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The Patagonian fossil mammal *Necrolestes*: a Neogene survivor of Dryolestoidea

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Abstract: *Necrolestes* is an enigmatic Miocene South American mammal that is the size of a shrew, the phylogenetic relationships of which constituted a matter of debate since its original description in 1891. This taxon has been variously related to the Chrysochloroidea, Palaeanodonta, Xenarthra, Gondwanatheria, and Metatheria. However, *Necrolestes* exhibits fossorial adaptations in combination with cranial, postcranial, and dental features that are remarkably plesiomorphic for a therian mammal. This led several authors to consider *Necrolestes* as a Theria *incertae sedis,* Tribosphenida *incertae sedis*, and even as a Mammalia *incertae sedis.* We present evidence in support that *Necrolestes* belongs to the Dryolestoidea, an extinct group of basal cladotherians that were abundant and widespread from the Late Jurassic through the Late Cretaceous. Recent discoveries demonstrated that the South American continent was a cradle for the evolutionary radiation of dryolestoid mammals at the end of the Cretaceous. Moreover, it become evident that some of these early mammals persisted across the K-P boundary, as illustrated by the peligrotheriid dryolestoid *Peligrotherium,* documented in Paleocene beds of Patagonia. A comprehensive cladistic analysis of living and fossil mammals depicts *Necrolestes* as a member of the dryolestoid subclade Meridiolestida, thus amplifying the morphological disparity of this lineage of southern dryolestoids, including dog-sized bunodontian forms (i.e., *Peligrotherium*), alongside with small-sized insectivores (i.e., *Necrolestes*). Present study solves the enigma that for the last 120 years surrounded the phylogenetic relationships of the bizarre mammal *Necrolestes*, also demonstrating the unexpected survival of South American dryolestoids up to Miocene times.

Key words: *Necrolestes*, Dryolestoidea, Meridiolestida, Miocene, Patagonia.

Resumen: El mamífero fósil *Necrolestes* de Patagonia: un superviviente Neógeno de los Dryolestoidea. *Necrolestes* es un enigmático mamífero del Mioceno de América del Sur del tamaño de una musaraña, cuyas relaciones filogenéticas han sido intensamente debatidas desde que fuera originalmente descripto en 1891 por Florentino Ameghino. Este taxón ha sido relacionado con los Chrysochloroidea, Palaeanodonta, Xenarthra, Gondwanatheria, y Metatheria. Sin embargo, *Necrolestes* exhibe adaptaciones fosoriales en combinación con caracteres craneanos, postcraneanos y dentarios remarcablemente plesiomórficos para un mamífero terio. Esto llevó a varios autores a considerar a *Necrolestes* como un Theria *incertae sedis,* Tribosphenida *incertae sedis*, e incluso como un Mammalia *incertae sedis.* Presentamos aquí evidencia anatómica que demuestra la pertenencia de *Necrolestes* a los Dryolestoidea, un grupo extinguido de cladoterios basales que fueron abundantes y ampliamente distribuidos durante el Jurásico Tardío al Cretácico Tardío. Descubrimientos recientes han demostrado que el continente Sudamericano constituyó una región clave en lo que respecta a la radiación evolutiva de los mamíferos driolestoideos hacia fines del Cretácico. Más aún, hoy se sabe que algunos de estos mamíferos arcaicos sobrepasaron la frontera Cretácico-Paleoceno, tal como es demostrado por el driolestoideo peligrotérido *Peligrotherium*, procedente de capas del Paleoceno de Patagonia. Un análisis comprehensivo de mamíferos vivientes y fósiles, llevado a cabo en el presente estudio, dio por resultado la inclusión de *Necrolestes* dentro del subclado driolestoideo de los Meridiolestida. Esto amplifica la disparidad morfológica conocida para este grupo de mamíferos australes, que incluyen animales bunodontes de la talla de un perro (i.e., *Peligrotherium*) hasta formas insectívoras y fosoriales de tamaño diminuto (i.e., *Necrolestes*). El presente estudio resuelve el enigma que durante los últimos 120 años rodeó las relaciones de parentesco del extraño *Necrolestes*, demostrando también la inesperada supervivencia de los driolestoideos sudamericanos hasta tiempos Miocenos.

Palabras clave: *Necrolestes*, Dryolestoidea, Meridiolestida, Mioceno, Patagonia.

INTRODUCTION

During the late early Miocene (Santacrucian Land Mammal age; 17 to 15 Ma) the South American continent reached its maximum of geographical isolation (Pascual & Ortíz Jaureguizar, 2007). By this time, Patagonia was populated by a high diversity of endemic land mammals, including metatherians, xenarthrans, South American native ungulates, caviomorph rodents, and primates Platyrrhini (e.g., Pascual, 2006; Pascual & Ortíz Jaureguizar, 2007). One of the most intriguing members of the Santacrucian fauna is the burrowing mammal *Necrolestes*, originally described by Argentine paleontologist Florentino Ameghino in 1891. *Necrolestes* was a minute mammal (skull length less than 35 mm) bearing peculiar postcranial traits interpreted as adaptations for a fossorial mode of life (e.g., stout and distally expanded humerus, ulna with modified olecranon, fused synsacrum; Scott, 1905; Asher *et al.,* 2007). More important, *Necrolestes* exhibits cranial, dental, and postcranial characteristics which are remarkably plesiomorphic for a therian mammal (e.g., unfused atlantal halves, non-interlocking molariforms; Asher *et al.,* 2007). Such a combination of highly autapomorphic and plesiomorphic characters lead authors to arrive to sharply different conclusions about the phylogenetic relationships of this Patagonian mammal. *Necrolestes* has been variously related to Chrysochloroidea (Scott, 1905), Palaeanodonta (Saban, 1954), Xenarthra (McDowell, 1958), Gondwanatheria (Van Valen, 1988), and Metatheria (Leche, 1907; Winge, 1941; Patterson, 1958; Szalay, 1994; Ladevèze *et al.,* 2008). It is evident that this genus does not comfortably fit in any of these well-known mammalian groups. In this regard, the remarkably primitive features present in *Necrolestes* led several authors to consider it as a Theria *incertae sedis* (McKenna & Bell, 1997), Tribosphenida *incertae sedis* (Reig, 1981), and even as a Mammalia *incertae sedis* (Asher & Sánchez-Villagra, 2005; Asher *et al.,* 2007; Goin *et al.,* 2007).

Probably because *Necrolestes* is a Miocene South American mammal, most comparisons were historically restricted to Cenozoic clades of Eutheria and Metatheria, but not with groups of more basal Mesozoic clades. Asher *et al.* (2007) conducted a careful comparative survey of *Necrolestes* with Metatheria, Eutheria, Gondwanatheria and Australophenida, but not with Dryolestoidea. However, a still growing body evidence demonstrates that by the end of the Cretaceous South America was inhabited by dryolestoid mammals (Bonaparte, 1990; 2002; Rougier *et al.,* 2009a,b; 2011), an extinct group of basal cladotherians that were abundant and widespread by Late Jurassic times on Laurasian continents (Kielan-Jawarowska *et al.,* 2004). Most important, and in sharp contrast with the mammalian evolutionary history that occurred in the northern continents, in South America the dryolestoids survived to the end-Cretaceous mass extinction, being recorded in lower Paleocene beds of central Patagonia (Gelfo & Pascual, 2001). Presence of dryolestoids in the Tertiary of South America invites to amplify comparisons of *Necrolestes* with more basal Mesozoic mammals, and particularly to test its affinities with dryolestoids.

Necrolestes is here included, for the first time, within a comprehensive cladistic analysis of living and fossil mammals. Below, we review those features previously interpreted as indicative of metatherian and therian affinities of *Necrolestes*, also analyzing derived characteristics that support its membership to the Dryolestoidea.

MATERIALS AND METHODS

Institutional abbreviations

MACN A, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina - National Ameghino Collection.

Reviewed material

MACN A-5742, incomplete left mandible (Holotype); MACN A-5743, incomplete right mandible; MACN A-5746, complete left radius; MACN A-5747, complete right femur; MACN A-5748, incomplete left femur; MACN A-5749, incomplete left pelvic girdle; MACN A-5750, complete right radio; MACN A-5751, complete right ulna; MACN A-10252: incomplete left mandible; MACN A-10253, canine; MACN A-10254, incisive tooth; MACN A-10256, incomplete left femur.

Cusp homology of molariform teeth in *Necrolestes*

In tribosphenic mammals the main lingual cusp of upper molars is the protocone. This cusp occludes in the talonid basin of lower molars (Kielan Jaworowska *et al.,* 2004). Because in *Necrolestes* a talonid basin is absent, previous authors (e.g., Patterson, 1958; Asher & Sánchez-Villagra, 2005; Asher *et al.,* 2007) unanimously agreed on the absence of a protocone cusp in

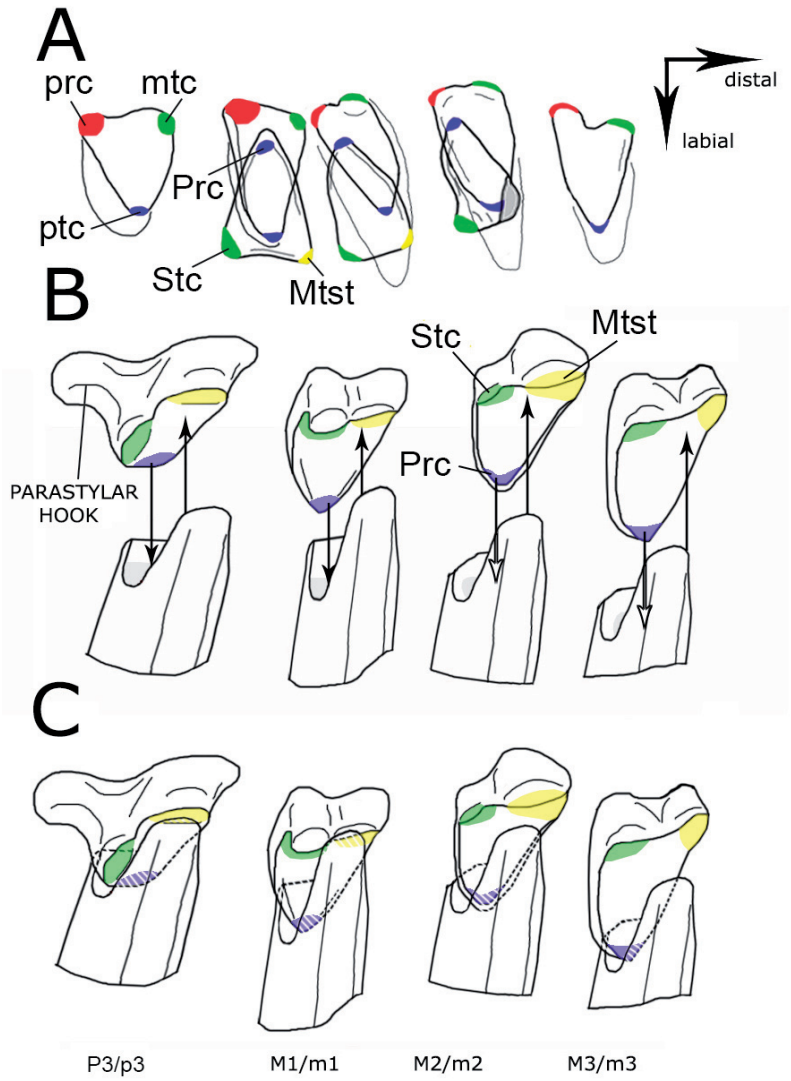

Fig. 1. Occlusal relationships of cusps in *Necrolestes* molariforms. **A**, oclusal view of lower molariforms (p2-m3) and its oclusal relationships with upper molariforms (P3-M2); **B**, labial view of the oclusal relationships among the P3/p3-M3/m3; **C**, labial view of the oclusal relationships among the P3/p3-M3/m3 in active occlusion. **Abbreviations:** Lower molariforms: mtc, metaconid; prc, paraconid; ptc, protoconid; Upper molariforms: Mtst, metastyle; Prc, paracone; Stc, stylocone. **Key colours of lower teeth:** red, paraconid; green, metaconid; blue, protoconid. **Key colours of upper teeth:** green, stylocone; yellow, metastyle; blue, paracone. **A-C** modified from Asher & Sánchez-Villagra (2005).

Necrolestes. It is worthy to mention that in the marsupial-mole *Notoryctes,* the only lingual cusp present in the upper molars was considered as a protocone, although a talonid basin is not present in lower molars (Archer *et al.,* 2011). However, the homologies of the main molar cusps in this living Australian marsupial are still a matter of debate, and work in progress may indicate different identities for each cusp (NRC pers. obs.). Thus, as explained above, although the dentition of *Necrolestes* is zalambdodont, it is clear that it does not have the occlusal cusp relationships characterizing zalambdodont tribosphenidans (Patterson, 1958; Asher & Sánchez-Villagra, 2005; Asher *et al.,* 2007). A point of contention concerns with the homology of the unusually large cusp that *Necrolestes* bears on the lingual side of its upper molars: Patterson (1958) referred this single lingual cusp as a presumable paracone; in contrast, Asher & Sánchez-Villagra (2005) and

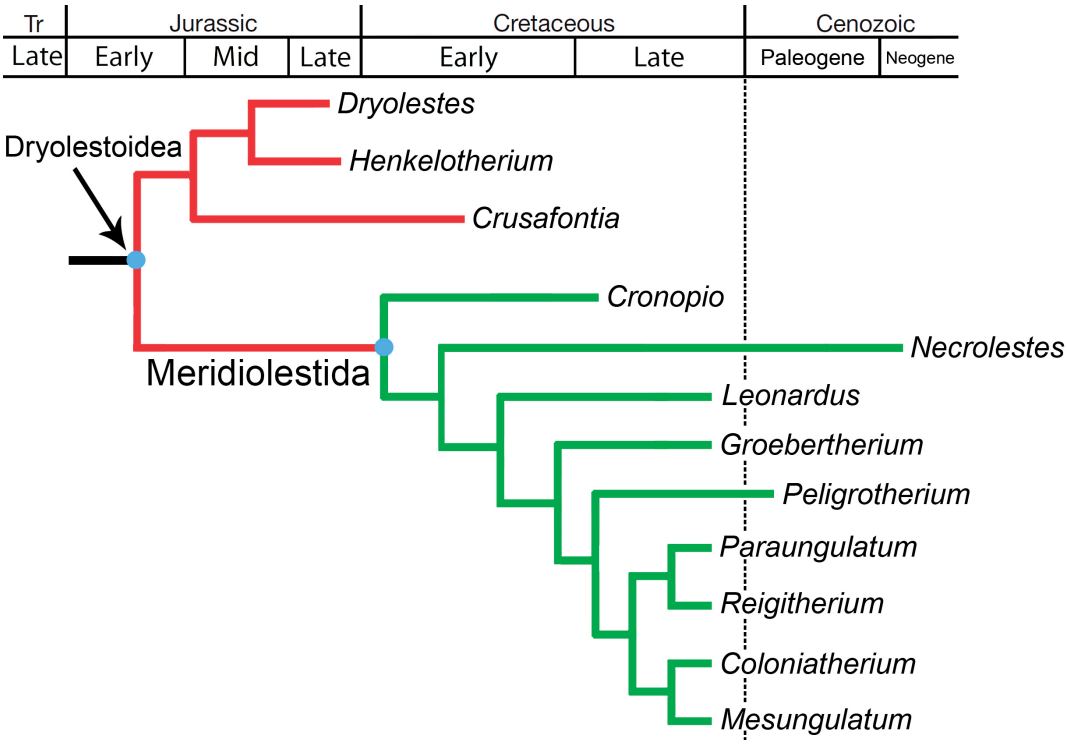

Fig. 2. Simplified cladogram of Dryolestoidea obtained in present phylogenetic analysis**.** Dryolestida is indicated in red color and Meridiolestida in green color. See Appendix 1-3 for complete data matrix, character list, character codification, and tree topology.

Asher *et al*. (2007) tentatively interpreted this main upper molariform cusp as the metacone. Probably, the main argument in support of the later identification is based on the assumption that *Necrolestes* is a member of Metatheria, a group of therians in which the main central cusp is the metacone. Moreover, Asher & Sánchez-Villagra (2005; see also Asher *et al.,* 2007) found support for such identification on the basis of the occlusal relationships between the main upper cusp (their metacone) and the paracristid of the more posterior lower molar. However, the main cusp of the upper molars results adjacent (in occlusion) to the lower ectoflexid of the respective more posterior lower molar, but not close to the paracristid (Fig. 1). Because the main cusp of the upper molars of *Necrolestes* does not occlude near the paracristid, it must be concluded that it is not a metacone. These occlusal relationships lend support to the identification of the main lingual cusp as the paracone. A source of information that contributes with this interpretation emerges from recently discovered Late Cretaceous dryolestoids from Patagonia. This is the case for *Cronopio* (Rougier *et al.,* 2011), which exhibits remarkable similarities in tooth morphology with *Necrolestes*. Such resemblance concerns with the simplicity in crown morphology, forming a triangle that bears three main cusps, with the lingual cusp (the paracone) being the largest, a condition shared by meridiolestidan dryolestoids (Gelfo & Pascual, 2001; Rougier *et al.,* 2011; Fig. 1).

Identification of the main lingual cusp of *Necrolestes* as the paracone affects the identification of the remaining secondary cusps of the upper molars: the mesiolabial small-sized cusp is identified as the stylocone (which connects with the paracone by means of a nearly transverse paracrista), and the distolabial secondary cusp is identified as the metastyle. Following previous authors, lower molariforms of *Necrolestes* bear a labial protoconid, a mesiolingual paraconid, and a distolingual metaconid (Patterson, 1958; Asher & Sánchez-Villagra, 2005).

Phylogenetic analysis

We present below a cladistic analysis of mammaliaform higher-level relationships, mostly based on the studies published by Luo *et al.*

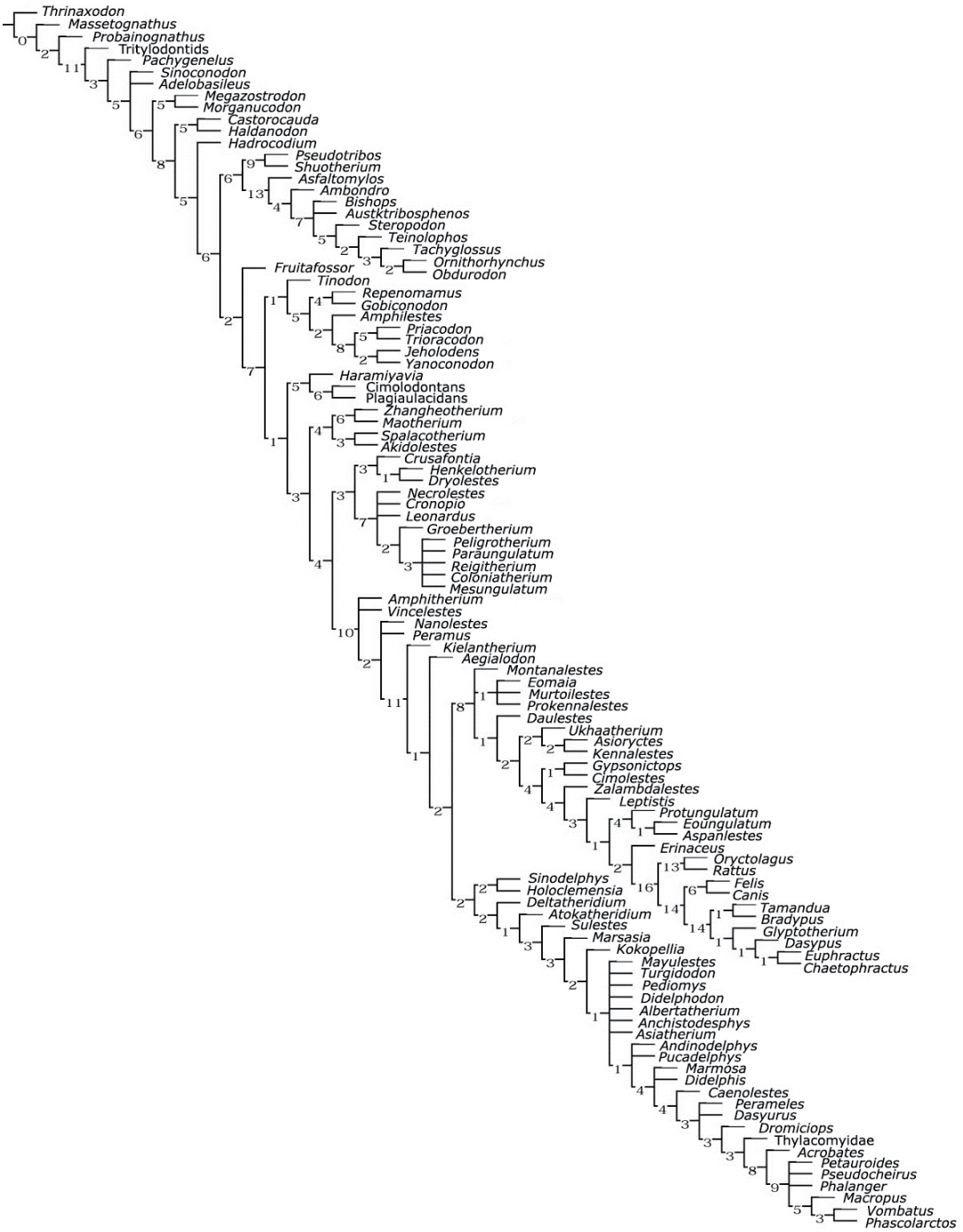

Fig. 3. Consensus tree of phylogenetic position for *Necrolestes* with Bremer support calculated for each node. The position of *Necrolestes* within dryolestoids remains as a robust phylogenetic signal (Bremer support = 3), and its inclusion within Meridiolestida conforms an extremely well-supported clade (Bremer support = 7).

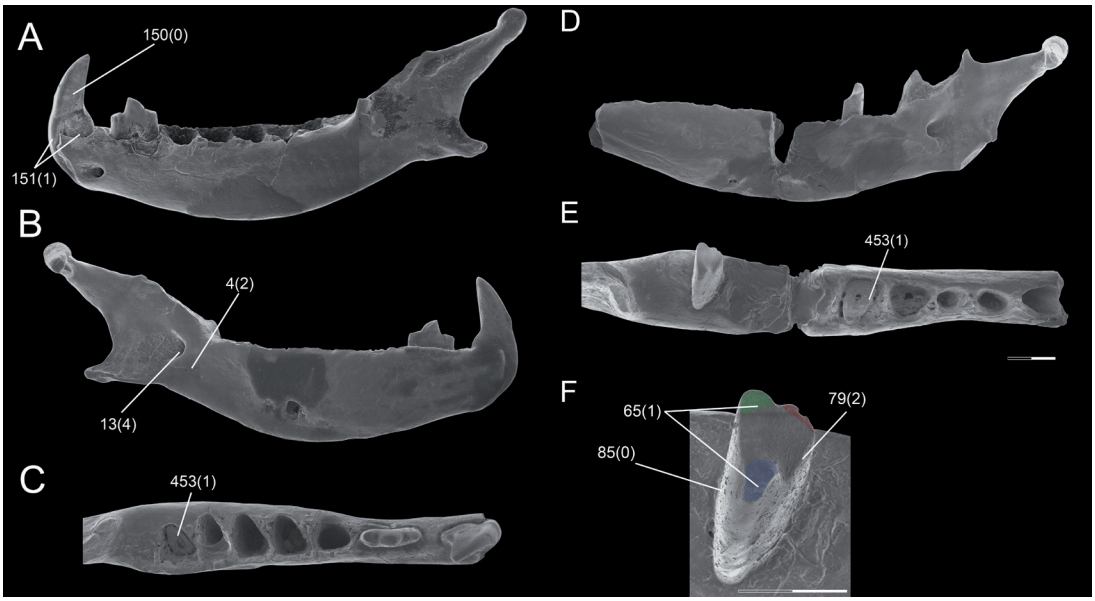

Fig. 4. *Necrolestes patagonensis* (MACN A-5742, holotype). **A-C**, left mandible in labial (A), lingual (B), and oclusal (C) views. **D-F**, right mandible in lingual (D) and occlusal (E) views, and m3 in oclusal view (F). Numbers refer to character number and state in the text, colors refer to different cusp positions. **Character numbers and states:** 4(2): meckelian sulcus absent; 13(4): wide mandibular foramen not associated with postdentary bones; 65(1), protoconid and metaconid subequal in size; 79(2), transverse paracristid; 85(0), talonid absent; 150(0), lower canine present and enlarged; 151(1), two lower canine roots; 453(1), mesiodistally compressed and transversely wide lower molar root. **Key colours:** green, paraconid; red, metaconid; blue, protoconid. Scale: 1 mm.

(2007). The data set was compiled including most characters traditionally used to diagnose Dryolestoidea, Metatheria, Marsupialia, and Australidelphia, among others. The data matrix is composed of 458 characters distributed among 113 taxa (Appendices 1 and 2). Most of the matrix used in the present study has been extracted from Luo *et al.* (2007), which compiled numerous morphological characters from previous contributions (e.g. Luo *et al.,* 2003; Luo & Wible, 2005). Following Bonaparte (2008), we have modified some codifications in Luo *et al.´s* (2007) data matrix. Characters 1-445 follow Luo *et al.* (2007; supplementary material) and characters 446-458 were added in the present analysis from different sources (i.e., Bonaparte, 1990; Chornogubsky, 2011; Rougier *et al.*, 2011). Following Bonaparte (1990), we modified character 104 from Luo *et al.* (2007) adding character-state 3. Codification of characters for *Necrolestes* follow published information from Scott (1905), Patterson (1958), Asher & Sánchez-Villagra (2005), Asher *et al.*(2007), Goin *et al.* (2007), and Ladevèze *et al.* (2008), as well as first-hand examination of holotype and referred specimens at MACN paleontological collection. Most features regarding braincase characters of *Reigitherium*, *Peligrotherium,* and *Cronopio* follow codifications from Páez Arango (2008) and Rougier *et al.* (2011). Postcranial characters of *Peligrotherium tropicalis* follow codifications in Rougier *et al.,* (2011). Codification of basicranial and inner ear characters of non-meridiolestidan dryolestoids follow Ruf *et al.* (2009), Rougier *et al.* (2009b), and Luo *et al.* (2011). We follow Chornogubsky (2011) in the interpretation of the holotype and referred specimens of *Leonardus*.

In order to drawn meaningful conclusions about "interordinal" relationships, and test the phylogenetic position of *Necrolestes* within a clear phylogenetic context, we choose 29 metatherian and 22 dryolestoid taxa as representatives of the major radiations within each of these clades.

The taxonomic nomenclature of the major clades follows that proposed by McKenna & Bell (1997), and nomenclature and classification among dryolestoids follows Martin (1999), with the modifications introduced by Kielan-Jaworowska *et al.* (2004) and Rougier *et al.,* (2011). We also follow tooth nomenclature and numeration employed by Luo *et al.* (2002), with the modifications introduced by Kielan-Jaworowska *et al.* (2004) and Luo *et al.* (2007).

The phylogenetic analysis was performed us-

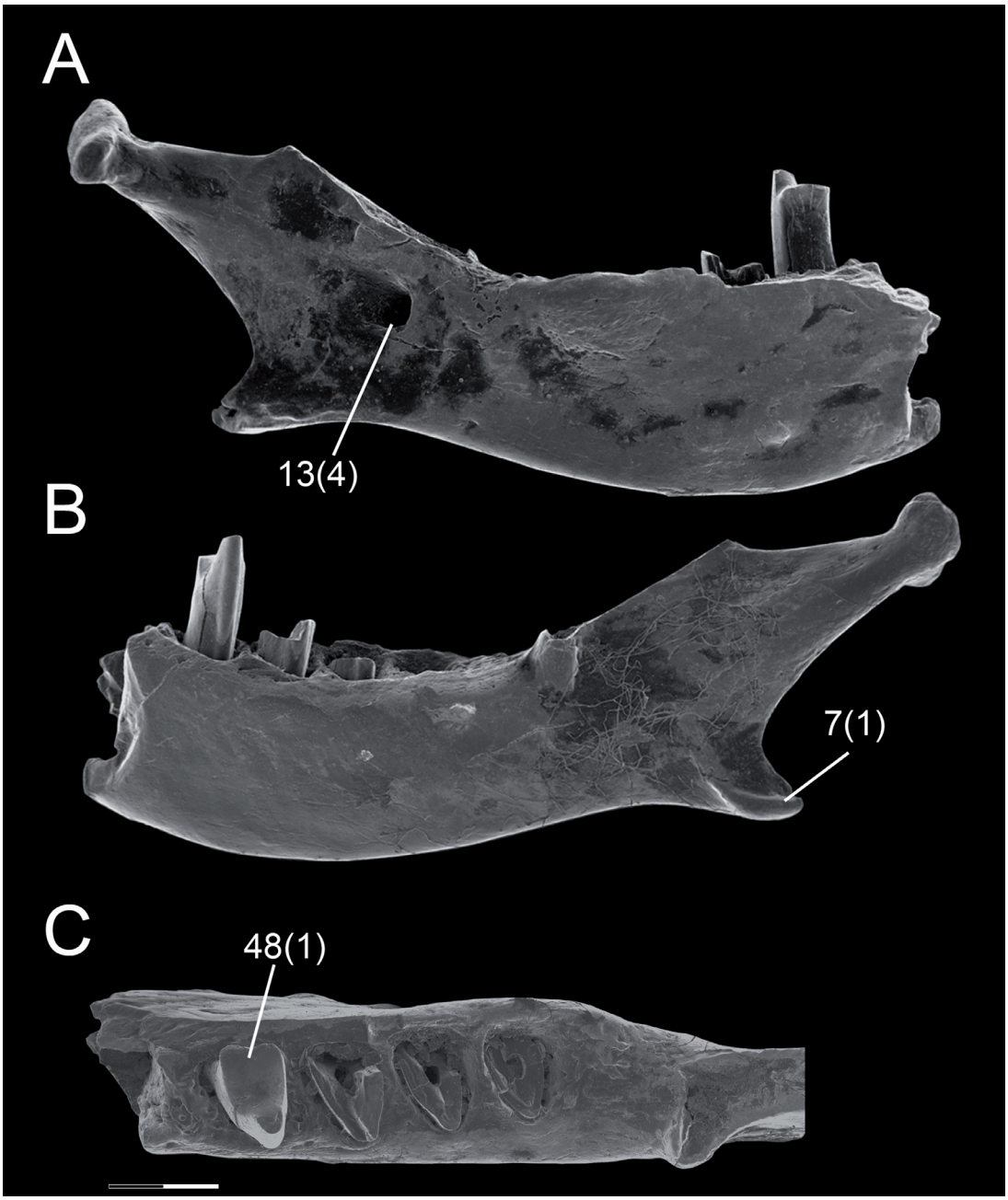

Fig. 5. *Necrolestes patagonensis* (MACN 10252). **A-C**, left mandible in lingual (A), labial (B) and occlusal views (C). Numbers refer to character number and state in the text. **Character numbers and states:** 7(1), angular process distinctive but not inflected; 13(4), wide mandibular foramen not associated with postdentary bones; 48(1), distinctive triangulation between the principal cusp a, cusp b and cusp c, of the ultimate lower premolar. Scale: 1 mm

ing TNT 1.1 (Goloboff *et al.*, 2008). All characters were equally weighted and treated as unordered. Heuristic searches were performed after 1,000 pseudoreplicates of WAG+TBR search strategy, with 10 random addition sequences after each search and 100 trees were saved at each replicate. The phylogenetic analysis resulted in the recovery of 140 Most Parsimonious Trees (MPTs), of 2365 steps, with a consistency index of 0.33, and a retention index of 0.793 (Fig. 2).

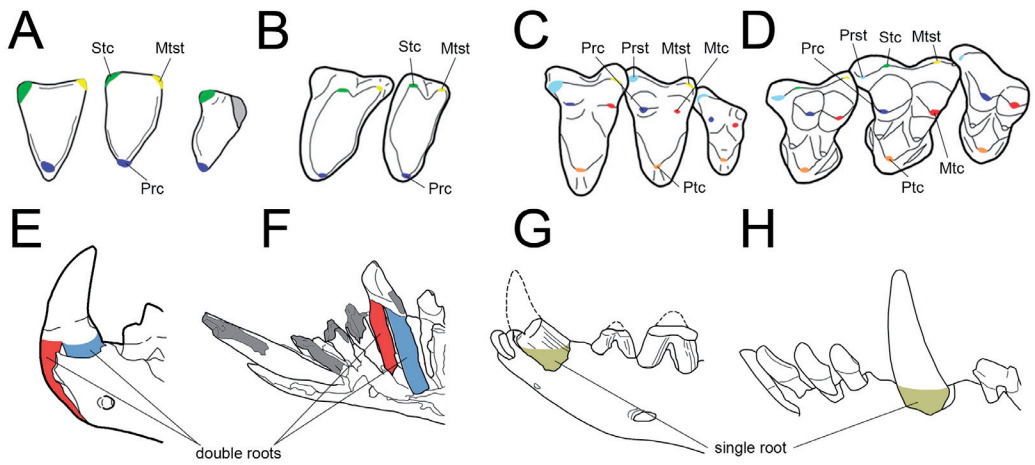

Fig. 6. Comparative figure showing main anatomical features discussed in the text, and its observed condition in *Necrolestes*. **A-D**, Left upper dentition of selected mammaliaforms. **A**, p3-m2 of *Necrolestes*; **B**, m1-m2 of *Cronopio*; **C**, m1-m3 of *Zalambdalestes*; **D**, m2-m4 of *Alphadon*. **Key colours:** green: stylocone; yellow: metastyle; blue: paracone; light blue: parastyle; red: metacone; orange: protocone. **E-H**, Anterior portion of left dentary in selected mammaliaforms, showing canine morphology. **E**, *Necrolestes*, in labial view (based in MACN 5742); **F**, *Dryolestes*, in lingual view; **G**, *Eodelphis*, in labial view; **H**, *Ukhaatherium*, in labial view. **Key colours:** red, anterior root; blue, posterior root; yellow, single-rooted. **Abbreviations:** cc, crus commune; ctpp, caudal tympanic process of petrosal; Mtc, Metacone; Mtst, metastyle; scc, secondary crus commune; sica, sulcus for the internal carotid artery; pc, prootic canal; Prc, paracone; Prst, parastyle; Ptc, protocone; Stc, Stylocone; pr, promontorium. Not to scale. A, modified from Asher & Sánchez-Villagra (2005); B, modified from Rougier *et al.* (2011); C, modified from Kielan-Jaworowska (1969); D, modified from Kielan-Jaworowska *et al.* (2004); F, modified from Martin (1999); G, modified from Matthew (1916); H, modified from Kielan-Jaworowska *et al.* (2004).

Robusticity tests

With the aim to test the robusticity of tree topology, we calculated the Templeton test and Bremer support for each node. Nesting of *Necrolestes* within Dryolestoidea is well supported (Bremer support =3), and its position within Meridiolestida is strongly supported (Bremer support =7), thus conforming a robust phylogenetic signal (Fig. 3).

To further test the robustness of the phylogenetic position of *Necrolestes* here recovered, a Templeton test for several of the alternative topologies was conducted. The test was performed following the protocol recently summarized by Wilson (2002). Different values were obtained, depending on the position of *Necrolestes*. The positions tested include: 1) *Necrolestes* at the base of Metatheria $p<0.0001$ (+52 steps); 2) *Necrolestes* as sister-group of Sparassodonta $p<0.0001$ (+58 steps); 3) *Necrolestes* as sister-group of Theria $p<0.0001$ (+52 steps); 4) *Necrolestes* at the base of Eutheria $p<0.0001$ (+56 steps); 5) *Necrolestes* at the base of the clade *Vincelestes*+Theria $p<0.0001$ (+28 steps); 6) *Necrolestes* at the base of Dryolestoidea $p=0.0015$ (+15 steps); 7) *Necrolestes* as the sister-group of the clade Dryolestoidea+Theria $p=0.0003$ (+24 steps); 8) *Necrolestes* at the base of Dryolestidae $p=0.0001$ (+17 steps); 9) *Necrolestes* at the base of Meridiolestida $p=0.6250$ (+2 steps); 10) *Necrolestes* at the base of the clade *Groebertherium*+Mesungulatoidea $p=0.5000$ (+2 steps); 11) *Necrolestes* as sister-group of Mesungulatoidea $p=0.0625$ (+5 steps); 12) *Necrolestes* at the base of Mesungulatidae $p=0.0020$ (+10 steps).

The smaller *P*-values are recovered when *Necrolestes* is placed within meridiolestidan dryolestoids. In contrast, a sister group position of *Necrolestes* and Metatheria is dismissed by the analysis with a confidence of 95% ($P = 0.029$, and thus < 0.05). In this way, the position of *Necrolestes* within Meridiolestida rests on robust evidence.

DISCUSSION

Although *Necrolestes* has been frequently considered a metatherian (Leche, 1907; Patterson, 1958; Asher *et al.*, 2007; Ladevèze *et al.*, 2008), some authors (e.g., Turnbull, 1971; Archer, 1984; Goin *et al.*, 2007) explicitly countered such taxonomic referral. In fact, *Necrolestes* is devoid of

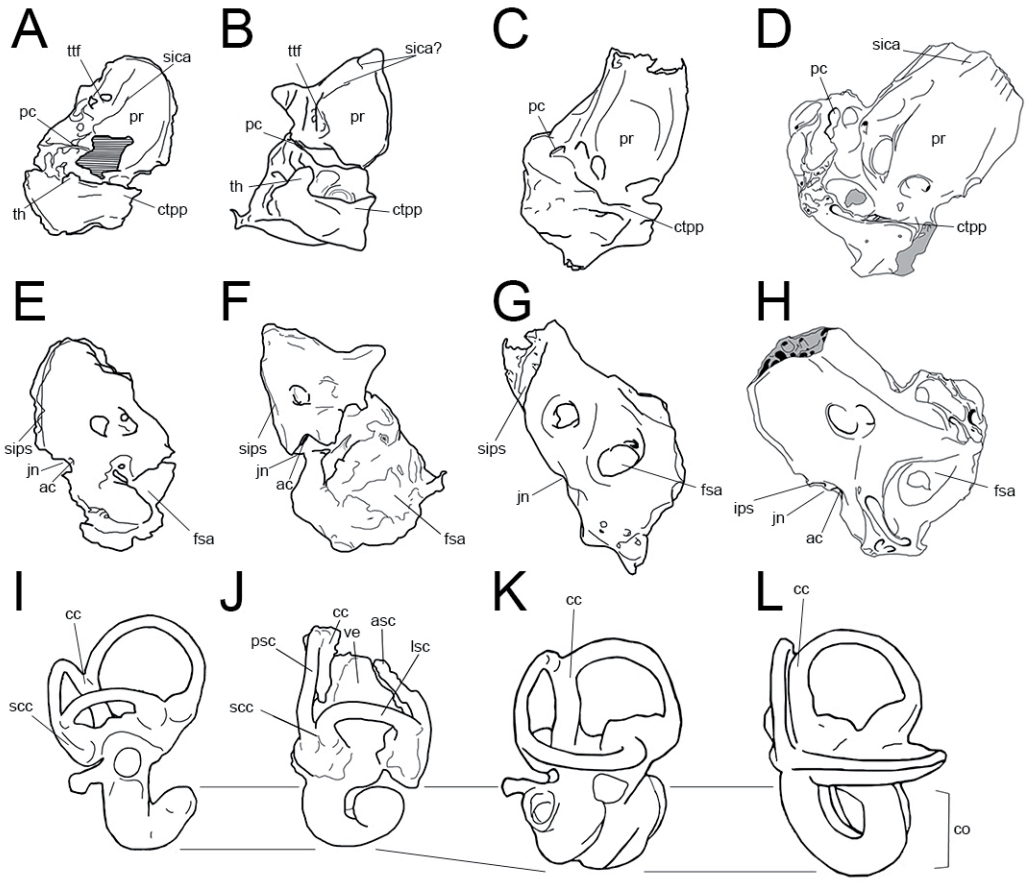

Fig. 7. Comparisons of petrosal and inner ear anatomy of selected mammals. **A-H**, right petrosal bones in **A-D**, ventral, and **E-H**, dorsal views. **A**,**E**, *Henkelotherium*; **B**,**F**, *Necrolestes*; **C**,**G** *Mimoperadectes*; **D**,**H**, *Prokennalestes*. **I-L,** right inner year in dorsal view. **I**, *Dryolestes*, **J**, *Necrolestes*, **K**, *Mimoperadectes*, **L**, *Adapis*. **Abbreviations:** ac, aqueductus cochleae; cc, crus commune; co, cochlea; ctpp, caudal tympanic process of petrosal; fsa, fossa subarcuata; ips, inferior petrosal sinus; jn, jugular notch; lsc, lateral semicircular canal; pc, prootic canal; pr, promontorium; psc, posterior semicircular canal; scc, secondary crus commune; ttf, tensor tympani fossa; ve, vestibule. Not to scale. A,E, modified from Ruf *et al.* (2009); B,F,J, modified from Ladevèze *et al.* (2008); C,G,K, modified from Horovitz *et al.* (2008); D,H, modified from Wible *et al.* (2001); I, modified from Luo *et al.* (2011); L, modified from Silcox *et al.* (2009).

several characteristics that are distinctive of metatherians and marsupials (e.g., Patterson, 1958; Asher *et al.,* 2007; Vullo *et al.,* 2009), such as fenestrated palate, alisphenoid forming a tympanic bulla (but see Muizón, 1994; 1998), similar sized and well-developed paracone and metacone, and large entoconid, among many other traits (Figs. 4, 5). Moreover, features of the inner ear that were recently recognized by Ladevèze *et al.* (2008) in support of the inclusion of *Necrolestes* within Metatheria (i.e., reduced prootic canal; location of inferior petrosal sinus bounded by petrosal, basisphenoid, and basioccipital; extrabullar location of internal carotid artery; loss of stapedial artery; and presence of caudal tympanic process on petrosal), exhibit a wider distribution than thought, being also documented in derived meridiolestidan dryolestoids (i.e., *Cronopio, Coloniatherium, Peligrotherium, Reigitherium*; Rougier *et al.* 2009a; 2011; Fig. 7). Besides, presence of a well-developed styloid process in distal ulna has been interpreted by Asher *et al.* (2007) as a derived feature uniting *Necrolestes* with Marsupialia, but this process has been also described for basal dryolestoids (i.e., *Henkelotherium*; Krebs, 1991).

Goin *et al.* (2007), on the basis of the dental replacement, concluded that *Necrolestes* may

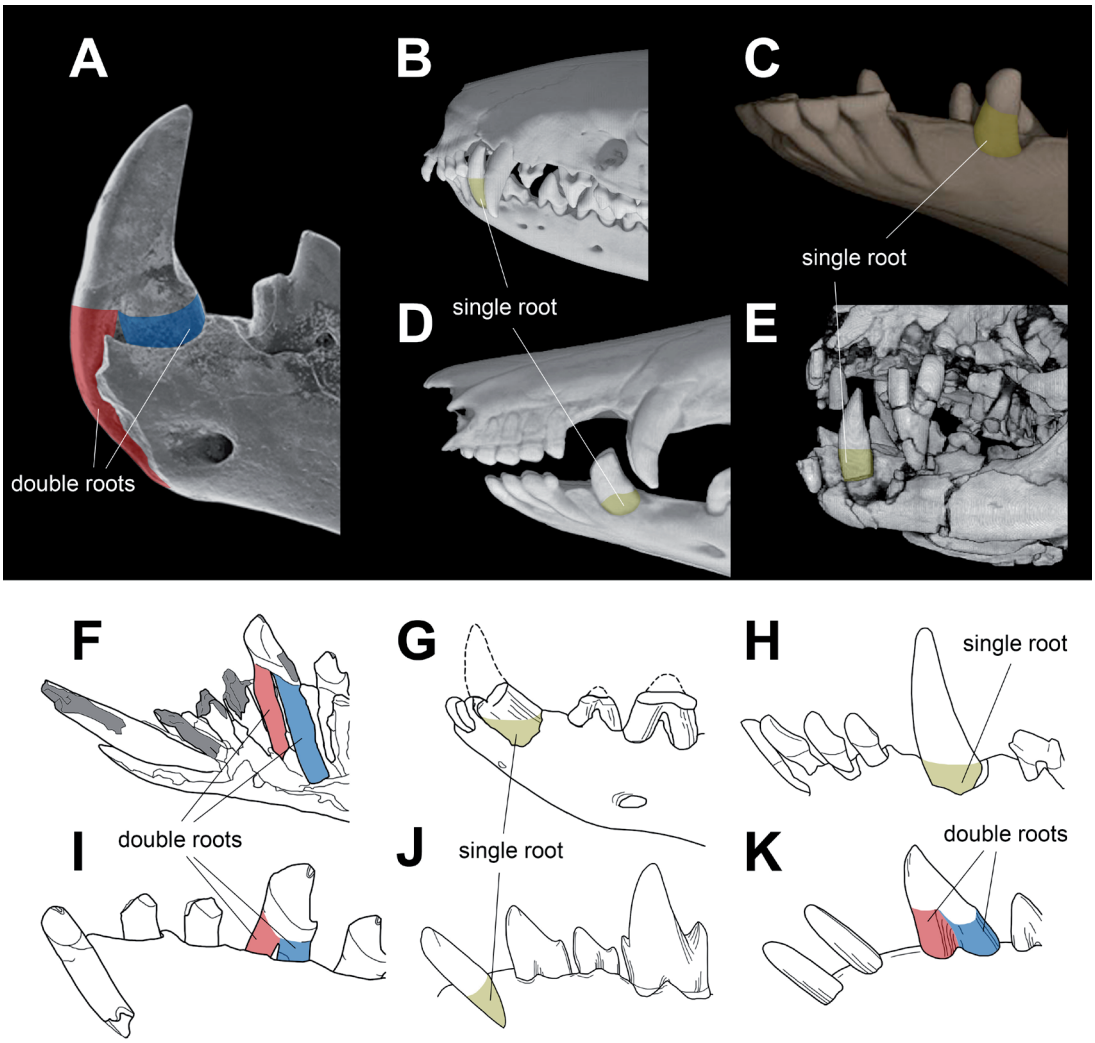

Fig. 8. Right dentaries of selected mammals showing anteriormost teeth indicating condition of canine roots. **A**, *Necrolestes* (Dryolestoidea); **B**, *Dasyurus* (Marsupialia); **C**, *Echymipera* (Marsupialia); **D**, *Macrotis* (Marsupialia); **E**, *Vincelestes* (Stem Theria); **F**, *Dryolestes* (Dryolestoidea); **G**, *Eodelphys* (Metatheria); **H**, *Ukhaatherium* (Eutheria); **I**, *Krebsotherium* (Dryolestoidea); **J**, *Zalambdalestes*; **K**, *Kennalestes* (Eutheria). **Key colours: yellow**, single canine root; **red** and **blue**, respective anterior and posterior roots of the canine tooth. Not to scale. A, MACN A-5742; B, modified from Macrini (2005); c, modified from Macrini (2008); D, modified from Macrini (2007); E, modified from Rowe (2001); F, I, modified from Martin (1999); G, modified from Matthew (1916); H, modified from Kielan-Jaworowska *et al.* (2004); J, K, modified from Kielan-Jaworowska (1969).

eventually have had affinities with extinct lineages of Theria, not referable either to Metatheria or Eutheria. Based on Goin *et al.* (2007) we conclude that the dental formula of *Necrolestes* is I 5/4, C 1/1, PM 3/3, M 3/3. The presence of three premolars and three molars has been reported in several meridiolestidans, including *Peligrotherium*, *Coloniatherium*, and *Cronopio* (Páez Arango, 2008; Rougier *et al.*, 2009a; 2011). In other poorly known meridiolestidans the presence of three molars has been also reported (e.g., *Leonardus*, *Reigitherium*, *Mesungulatum*; Rougier *et al.*, 2011). In fact, *Necrolestes* lacks most of the derived features characterizing therian mammals: from the 12 therian synapomorphies ennumerated by Asher *et al.* (2007), only three of them (i.e., presence of astragalar neck, fully coiled cochlea of inner ear, and absence of septomaxilla) are present in *Necrolestes*. Nevertheless, these characters are problematic.

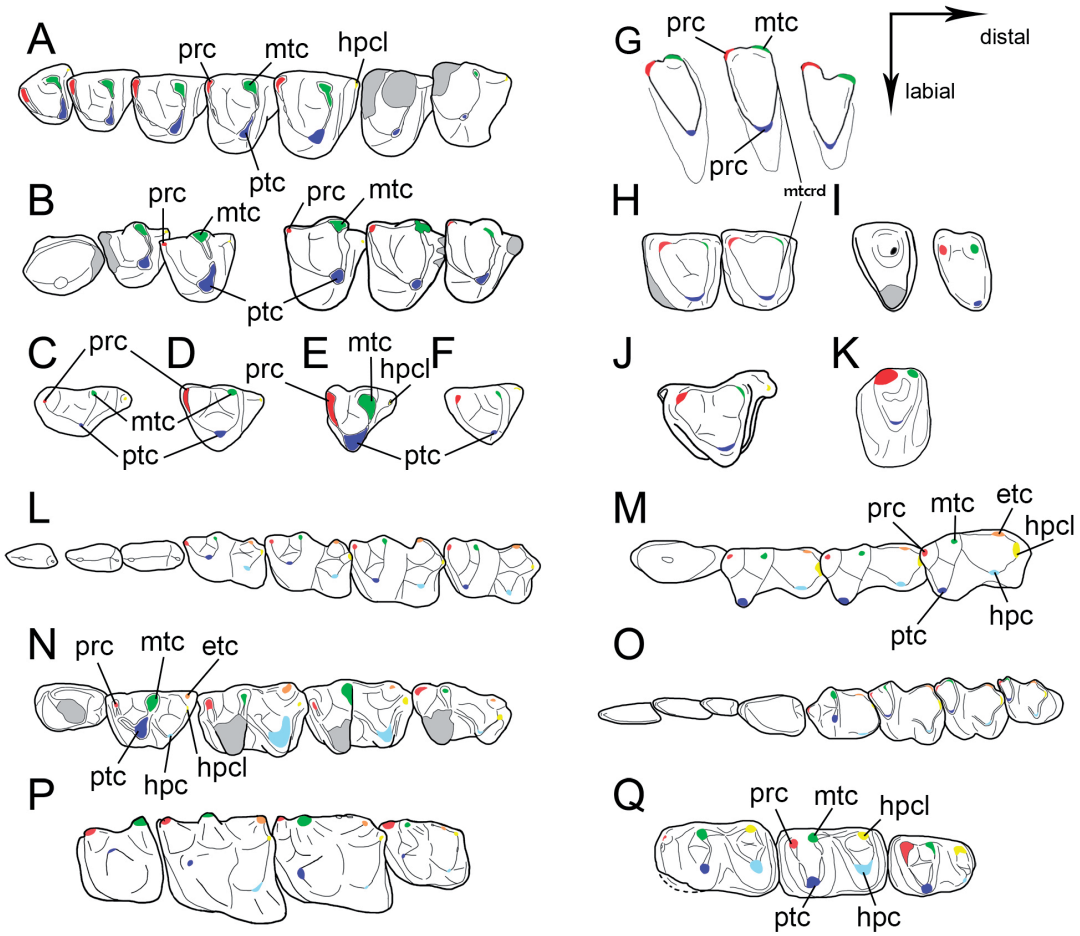

Fig. 9. Lower dentitions of selected mammaliaforms in oclusal view. **A**, m1-m7 of *Dryolestes* (Dryolestoidea); **B**, p4-m2 and m5-m8 of *Guimarotodus* (Dryolestoidea); **C**, ?m of *Chunnelodon* (Dryolestoidea); **D**, ?m of *Tathiodon* (Dryolestoidea); **E**, ?m of *Laolestes* (Dryolestoidea); **F**, ?m of *Amblotherium* (Dryolestoidea); **G**, p2-m3 of *Necrolestes* (Dryolestoidea); **H**, p4-m1 of *Mesungulatum* (Dryolestoidea); **I**, two molars of *Leonardus* (Dryolestoidea); **J**, ?m of *Brandonia* (Dryolestoidea); **K**, ?m of *Coloniatherium* (Dryolestoidea); **L**, p3-m4 of *Asiatherium* (Metatheria); **M**, p4-m3 of *Prokennalestes* (Eutheria); **N**, p3-m4 of *Alphadon* (Metatheria); **O**, dentition of *Zalambdalestes* (Eutheria); **P**, p4-m3 of *Aukstribosphenos* (Australosphenida); **Q**, m1-m3 of *Steropodon* (Australosphenida). **Abbreviations:** etc, entoconid; hpc, hypocone; hpcl, hypoconulid; mtc, metaconid; mtcrd, metacristid; prc, paraconid; ptc, protoconid. **Key colours: blue**, protoconid; **red**, paraconid; **green**, metaconid; **yellow**, hipoconulid; **orange**, entoconid; **light blue**, hipoconid. Not to scale. A, B, E, modified from Martin (1999); C, D, F, H, L-O, modified from Kielan-Jaworowska *et al.* (2004); G, modified from Asher & Sánchez-Villagra (2005); I, modified from Chornogusky (2011); K, modified of Rougier *et al.* (2009b); P, modified from Rich *et al.* (2002); Q, modified from Luo *et al.* (2002).

For example, an astragalar neck was reported by Scott (1905), but the astragalus was never illustrated and it is currently lost (Asher *et al.*, 2007). Thus, the astragalar morphology cannot be analyzed in *Necrolestes* and checking of such character is forbidden. Regarding the cochlea, it is represented in *Necrolestes* by a broad and hollow tube of uniform diameter, coiled by 1.1 spiral turns (Ladevèze *et al.*, 2008). In contrast, all therian mammals show a fully coiled cochlea, and none of them has a cochlear coiling of less than 1.4 spiral turns (Ladevèze *et al.*, 2008; Fig. 7). A poorly coiled cochlea is also present in basal mammals, including *Vincelestes*, basal dryolestoids (i.e., *Dryolestes, Henkelotherium*; Ruf *et al.*, 2009; Luo *et al.*, 2011), and basal meridiolestidans (i.e., *Cronopio*; Rougier *et al.*, 2011). Additionally, some derived meridiolestidans possess fully coiled cochlea (more of 1 spiral turn), including *Peligrotherium*, *Reigitherium* and

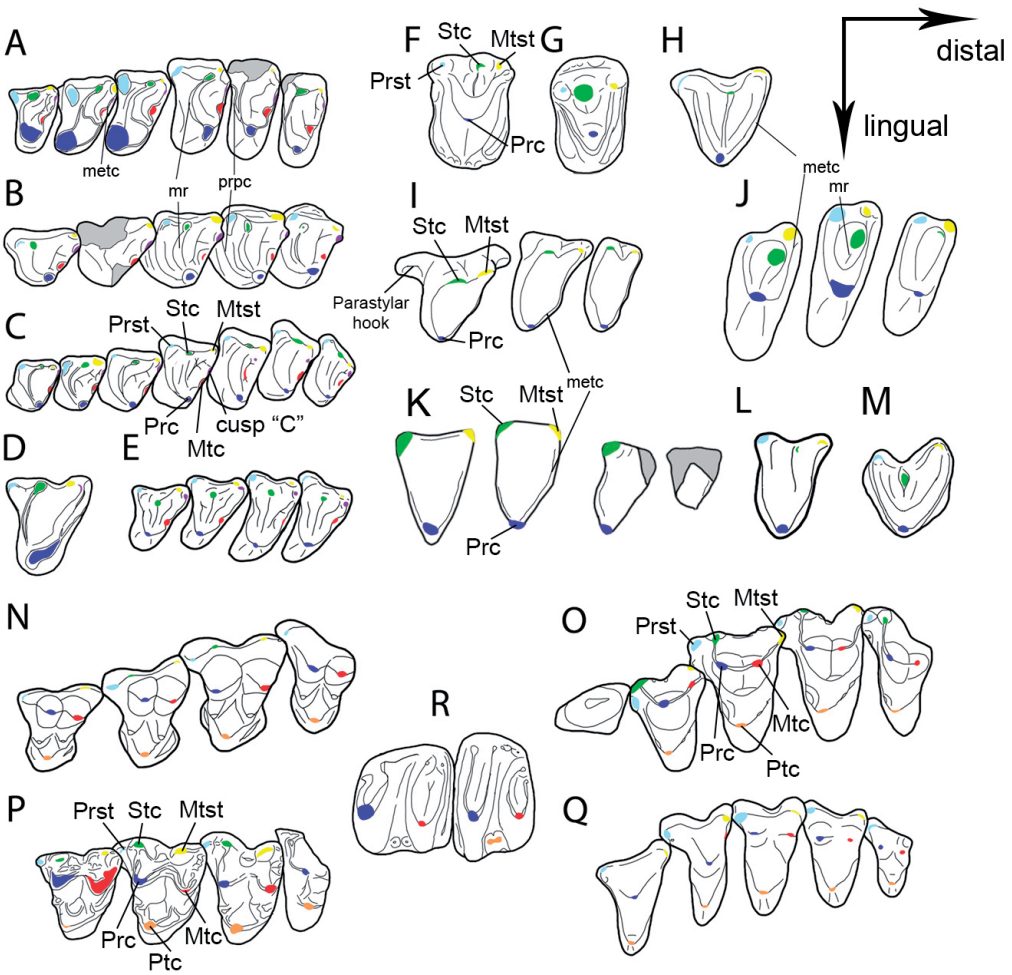

Fig. 10. Upper dentitions of selected mammaliaforms in oclusal view. **A**, M1-M7 of *Dryolestes* (Dryolestoidea); **B**, M1-M5 of *Henkelotherium* (Dryolestoidea); **C**, M1-M7 of *Krebsotherium* (Dryolestoidea); **D**, ?M of *Crusafontia* (Dryolestoidea); **E**, ?M of *Laolestes* (Dryolestoidea); **F**, ?M3 of *Mesungulatum* (Dryolestoidea); **G**, ?M3 of *Coloniatherium* (Dryolestoidea); **H**, ?M of *Brandonia* (Dryolestoidea); **I**, P4-M2 of *Cronopio* (Dryolestoidea) ; **J**, ?M1-3 of *Leonardus* (Dryolestoidea); **K**, P3-M3 of *Necrolestes* (Dryolestoidea); **L**, ?M of *Groebertherium* (Dryolestoidea); **M**, ?M of *Casamiquelia* (Dryolestoidea); **N**, M1-M4 of *Asiatherium* (Metatheria); **O**, P3-M3 of *Prokennalestes* (Eutheria); **P**, M1-M4 of *Alphadon* (Metatheria); **Q**, R, P3-M3 of *Zalambdalestes* (Eutheria), **R**, M1-M2 of *Obdurodon* (Monotremata). **Key colours: blue**, paracone; **red**, metacone; **green**, stylocone; **yellow**, metastyle; **light blue**, parastyle; **orange**, protocone; **violet**, cusp "C". **Abbreviations:** Mtc, metacone; metc, metacrista; mr, median ridge; Mtst, metastyle; Prc, paracone; prpc, preparacrista; Prst, parastyle; Ptc, protocone; Stc, stylocone. Not to scale. A, C, modified from Martin (1999); B, D, E, N, O, P, Q modified from Kielan-Jaworowska *et al.* (2004); F, modified from Rougier *et al.* (2009a); G, modified from Rougier *et al.* (2009b); H, L, M modified from Bonaparte & Migale (2010); I, modified from Rougier *et al.* (2011); J, modified from Chornogusky (2011); K, modified from Asher & Sánchez-Villagra (2005); M, modified from Bonaparate & Migale (2010); R, modified from Luo *et al.* (2002).

Coloniatherium (Páez Arango, 2008; Rougier *et al.,* 2009a; 2011). In consequence, the cochlear morphology of *Necrolestes* approaches more to the plesiomorphic mammalian condition rather than to the eutherian and metatherian molds. Finally, although we follow Asher *et al.* (2007) in the codification of the absence of septomaxilla as a synapomorphy uniting *Necrolestes* with Theria, it is worth mention that bones of the skull roof in *Necrolestes* are tightly fused (Patterson, 1958; Asher *et al.,* 2007), thus the recognition of a septomaxilla may be regarded as uncertain.

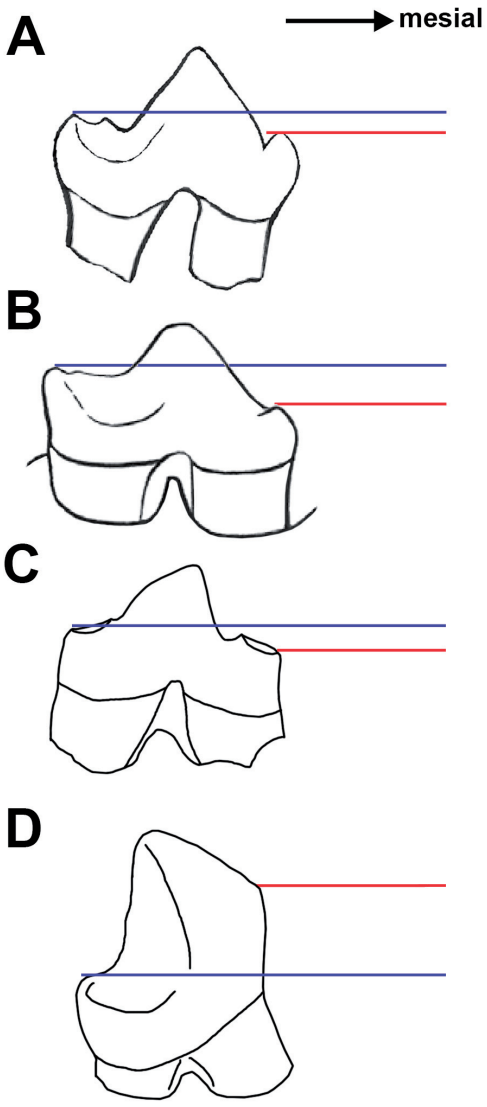

Fig. 11. Lower anterior premolar of selected dryolestoids in labial view. **A**, isolated premolar of *Austrotriconodon mckennai*; **B**, p2 of *Cronopio dentiacutus*; **C**, p1 of *Necrolestes patagonensis*; **D**, *Krebsotherium lusitanicum*. Not to scale. **References:** Red bar indicates the position of the mesial cusp; Blue bar indicates the position of distal cusp. A, modified from Bonaparte (1986); B, modified from Rougier *et al.* (2011); C, based in MACN A-5742; D, modified from Martin (1999).

Synapomorphies nesting *Necrolestes* within Dryolestoidea

Necrolestes shares with Dryolestoidea the following unambiguous synapomorphies:

1. Double-rooted lower canines (character 151-1). In most basal mammals, such as Eutriconodonta (e.g. *Amphilestes*, *Priacodon*, *Triconodon*), *Gobiconodon*, Multituberculata (e.g. Paulchoffatiidae and Pinheirodontidae), and *Kuehneotherium*, the upper and lower canines are single-rooted (Figs. 6, 8). All metatherians have retained this plesiomorphic condition (Kielan-Jaworowska *et al.,* 2004). In basal eutherians the condition of the canine is variable, some taxa exhibiting single-rooted lower canines (as in the case of *Eomaia*, *Zalambdalestes*, *Barunlestes* and *Ukhaatherium*; Kielan-Jaworowska 1969; Kielan-Jaworowska & Trofimov, 1980; Novacek *et al.,* 1997; Ji *et al.,* 2002), whereas in others (e.g., *Asioryctes*, *Prokennalestes*, *Kennalestes*; Kielan-Jaworowska, 1969; Kielan-Jaworowska, 1981; Kielan-Jaworowska & Trofimov, 1981; Kielan-Jaworowska *et al.,* 2004) a double-rooted canine is present. Double-rooted canines are also documented in spalacotheroid symmetrodonts (Tsabumoto *et al.,* 2004; Kielan-Jaworowska *et al.,* 2004), as well as in all known Dryolestoidea (Clemens & Lillegraven, 1986; Martin, 1997; 1999; Kielan-Jaworowska *et al.,* 2004; Rougier *et al.,* 2009b; 2011), including the meridiolestidans *Peligrotherium*, *Coloniatherium*, and *Cronopio* (Páez Arango, 2008; Rougier *et al.,* 2009a; 2011). *Necrolestes* possesses double-rooted upper and lower canines, with both roots well developed (Asher *et al.,* 2007; Fig. 8). In the present cladistic analysis, the presence of double rooted canines is recovered as a synapomorphy uniting *Necrolestes* with the remaining dryolestoids.

2. Protoconid and metaconid subequal in height (character 65-1). Traditionally, a typical synapomorphic trait of Metatheria is the presence of a reduced metaconid on the lower molars, which is at least 30% smaller than the protoconid (see Asher *et al.,* 2007). However, this condition is not seen in *Necrolestes*, in which both metaconid and protoconid are subequal in height (Asher & Sánchez-Villagra, 2005), the metaconid being less than 5% smaller than the protoconid (Figs. 1, 9). This morphology is also reported in most dryolestoids in which dentitions are well-known, including *Dryolestes, Henkelotherium,* and the bunodont taxa *Peligrotherium* and *Mesungulatum* (Bonaparte, 1986; Martin, 1999; Gelfo & Pascual, 2001).

3. Absence of distal metacristid in lower molariforms (character 136-1). The talonid (or pseudotalonid) of lower molars in mammals usually exhibits a ridge uniting the entoconid with the metaconid cusp of the trigonid (Fox, 1975; Kielan-Jaworowska *et al.,* 2004). This ridge is termed distal metacristid (Kielan-

Jaworowska *et al.,* 2004), and it is present in several Mesozoic lineages, including "peramurids", *Kielantherium*, and Deltatheridia. This feature is considered a diagnostic trait of the clade Zatheria, although it has been lost in some marsupials (Sigogneau-Russell, 1999; Kielan-Jaworowska *et al.,* 2004; Lopatin & Averianov, 2007). In basal Dryolestoidea a well-developed talonid (or pseudotalonid) and a distal metacristid are absent (Kielan-Jaworowska *et al.,* 2004; Rougier *et al.,* 2011). In available lower molars of *Necrolestes* both the talonid and the distal metacristid are also absent (Figs. 4, 5, 9), a condition that is here recovered as a synapomorphy supporting inclusion of *Necrolestes* within Dryolestoidea.

4. Prootic canal present, but reduced and horizontally positioned (character 325-2). Ladevèze *et al.* (2008) sustained the metatherian affinities of *Necrolestes* on the basis of several characters corresponding to the ear-region. One of these traits is a reduced prootic canal horizontally oriented, a condition present in *Necrolestes* (Asher *et al.,* 2007; Ladevèze *et al.,* 2008; Figs. 6, 7). However, such condition is not unique of metatherians, being also reported for basal dryolestoids (i.e., *Henkelotherium*; Ruf *et al.,* 2009) as well as meridiolestidans (i.e., *Coloniatherium, Reigitherium, Peligrotherium, Cronopio*), in which the prootic canal is reduced and horizontally oriented (Rougier *et al.,* 2009b; 2011). This condition is indistinguishable from that exhibited in *Necrolestes*. In the present analysis a reduced prootic canal emerges as a diagnostic feature of Dryolestoidea (including *Necrolestes*), that was convergently acquired by metatherians.

5. Secondary crus commune at the semicircular canals of the inner ear (character 458-1). The secondary crus commune constitutes a point of the inner ear at which the posterior semicircular canals cross-over the lateral one (Ladevèze *et al.,* 2008; Figs. 6, 9). This peculiar morphology is only present in selected therian mammals, including derived didelphids, dasyurids, and some eutherian genera (Schmelzle *et al.,* 2007; Ladevèze *et al.,* 2008; Luo *et al.,* 2011). Ladevèze *et al.* (2008) indicated the presence of this condition in *Necrolestes* and in some Metatheria. However, this morphology of the semicircular canals has been also recently reported by Luo *et al.* (2011) for the dryolestoids *Dryolestes* and *Henkelotherium* (see also Ruf *et al.,* 2009). In the present analysis, the existence of a secondary crus commune is better supported as a synapomorphy uniting *Necrolestes* with dryolestoids, and convergently acquired by some selected therians.

6. Shallow and weakly developed patellar groove of femur (character 244-1). In basal mammaliaforms, as well as in monotremes, the distal end of femur is anteriorly flat and lacks any sign of patellar groove (Jenkins & Parrington, 1976; Forasiepi & Martinelli, 2003). A similar morphology is seen in some arboreal metatherians, including didelphids, *Dromiciops*, and the extinct *Asiatherium* (Chester *et al.,* 2012). In contrast, in multituberculates, as well as in therians, the patellar groove on distal femur is deeply excavated and its medial and lateral edges are bounded by sharp bony ridges (see Forasiepi & Martinelli, 2003; Chester *et al.,* 2010). In *Necrolestes*, as well as in the basal dryolestoid *Henkelotherium*, the distal end of femur lacks a well-developed and defined patellar groove on its anterior surface; instead, a shallow and poorly defined patellar groove is present in both *Henkelotherium* and *Necrolestes* (Krebs, 1991; Asher *et al.,* 2007; Fig. 10). The morphology is still unknown for the remaining dryolestoids. In the context of the available evidence, an incipient patellar groove on distal femur is considered as a derived feature diagnostic of Dryolestoidea, including *Necrolestes*.

Necrolestes exhibits the following six synapomorphic characters of the dryolestoid clade Meridiolestida:

1. Triangulation of cusps a, b and c of the last lower premolar (Character 48-1). Basal mammaliforms (e.g., Morganucodonta, "Symmetrodonta", "Docodonta"; Kielan-Jaworowska *et al.,* 2004) exhibit a distinctive morphology of the premolars (and molars), given by the presence of the main cusps (i.e., cusps a, b and c), mesiodistally aligned. Albeit in different clades of mammals such plesiomorphic pattern was rearranged with the acquisition of a tribosphenic structure (Kielan-Jaworoswska *et al.,* 2004), premolars still retained their original cusp alignment. In some Eutheria, most posterior premolars acquired an occlusal morphology similar to the molars, whereas most metatherians lack molarized premolars (Kielan-Jaworoska *et al.,* 2004). In basal dryolestoids (e.g., *Dryolestes*, *Henkelotherium*) the last premolar is non-molarized, thus retaining the plesiomorphic mesiodistal cusp arrangement (Krebs, 1991; 1998; Martin, 1999; Kielan-Jaworowska *et al.,* 2004). In contrast, in the dryolestoids Meridiolestida and Paurodontidae the last premolars are very

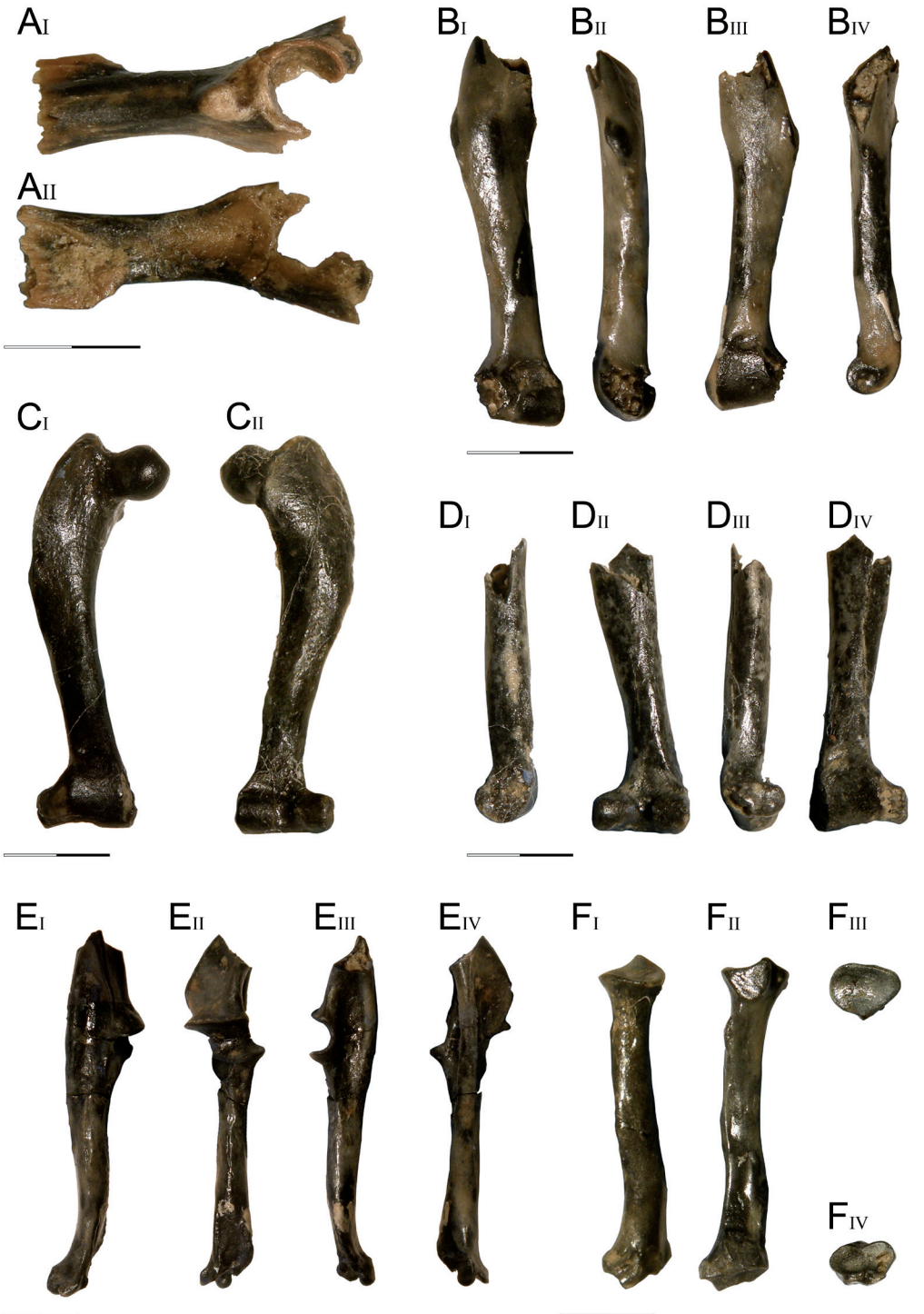

Fig. 12. Post-cranial remains of *Necrolestes patagonensis*. **A**, left pelvic girdle (MACN A-5749) in lateral (I), and medial views (II); **B**, left femur (MACN A-5748) in posterior (I), lateral (II), anterior (III), and medial views (IV); **C**, right femur (MACN A-5747) in anterior (I), and posterior views (II); **D**, left femur (MACN A-10256) in posterior (I), lateral (II), anterior (III), and medial views (IV); **E**, right ulna (MACN A-5751) in lateral (I), anterior (II), medial (III), and posterior views (IV); **F**, left radius (MACN A-5746) in anterior (I), posterior (II), proximal (III), and distal views (IV). Scale bar 4 mm.

similar to the molars, having a molarized crown with a triangular disposition of cusps (Rougier *et al.,* 2011). Furthermore, in meridiolestidans not only the last premolar, but also the penultimate one, are molarized (e.g. *Coloniatherium*, *Cronopio*; Rougier *et al.,* 2011). In *Necrolestes*, the first premolar retains the plesiomorphic alignment of the main cusps, but the second and third (last) premolars acquired the triangular disposition of cusps a, b and c, thus constituting a derived condition that *Necrolestes* shares with the remaining meridiolestidans (Figs. 4, 5, 6, 9).

2. Talonid absent (Character 85-0). The talonid is a neoformation of tribosphenic mammals (Sigogneau-Russell, 1998; Kielan-Jaworowska *et al.,* 2002), although many authors have established the presence of talonid (or "pseudotalonid") in different non-tribosphenic mammalian groups (Kermack *et al.,* 1987; Luo *et al.,* 2001; Luo *et al.,* 2007; Luo, 2007). In basal dryolestoids, such as *Henkelotherium*, *Foxraptor*, *Crusafontia* and *Dryolestes*, the talonid is reduced, being represented only by a small-sized shelf carrying a small cusp that is usually considered as the hypoconulid (Schultz & Martin, 2011). In more derived dryolestoids, including all meridiolestidans (e.g., *Leonardus*, *Cronopio*; Bonaparte, 1990; Chornogubsky, 2011; Rougier *et al.,* 2011) the talonid is totally absent, a condition interpreted as a derived feature of meridiolestidans (Rougier *et al.,* 2011) (Figs. 4-6, 9). This character state is also observed in *Necrolestes*, in which the talonid is totally absent (Asher & Sánchez-Villagra, 2005; Asher *et al.,* 2007; Figs. 4-6, 9).

3. Metastylar lobe much larger than the parastylar lobe (Character 121-2). In several mammaliform groups, including most eupantotherian and tribosphenic mammals (Kielan-Jaworowska *et al.,* 2004), the parastylar lobe carries one of the main lingual cusps, the parastylar cusp. In basal Dryolestoidea (e.g., *Dryolestes*, *Crusafontia*; Krebs, 1993; Martin, 1999; Cuenca-Bescós *et al.,* 2011) the parastylar lobe is well developed, being larger than the metastyle, forming a hook-like projection. In contrast, in all Meridiolestida the parastyle is reduced and the metastyle is larger than the parastyle (Rougier *et al.,* 2011). In mesungulatoid meridiolestidans the parastyle and the parastylar hook are highly reduced or absent (Rougier *et al.,* 2009a; 2009b; 2011), while in the basal meridiolestidans *Cronopio* and *Leonardus* the posterior molars are totally devoid of a parastyle, and the stylocone and metastyle are the only labial cusps present in each tooth (Chornogubsky, 2011; Rougier *et al.,* 2011; Figs. 6, 11). Similarly to *Cronopio*, *Leonardus*, and mesungulatoids, *Necrolestes* is devoid of parastyle, a feature here considered diagnostic of Meridiolestida.

4. Upper molariforms lacking metacone (Character 104-3). The metacone is a neoformation in the upper molars of "eupantotherian" mammals (Crompton, 1971; Kielan-Jaworowska *et al.,* 2004). In most dryolestids (e.g. *Dryolestes*, *Laolestes*, *Tathiodon*, *Henkelotherium*; Krebs, 1991; Martin, 1999; Kielan-Jaworowska *et al.,* 2004) the metacone is represented by a small centrodistal cusp located near cusp "C", both being connected through a metacrista (Krebs, 1991; Martin, 1999; Schultz & Martin, 2011). In Meridiolestida, the metacone is totally absent, as observed in all known mesungulatids, including the specialized genera *Peligrotherium* and *Paraungulatum* (Gelfo & Pascual, 2001; Bonaparte, 2002; Figs. 6, 11). In *Necrolestes* the occlusal surface is constituted by the stylocone, paracone and metastyle, with the total absence of a metacone. The absence of this cusp is hypothesized as a synapomorphy that unites *Necrolestes* with Meridiolestida.

5. Lower molar roots mesiodistally compressed and transversely wide (Character 453-1). In basal dryolestoids, as occurs in the majority of mammals, the roots of lower molariform roots are subcircular to ellipsoidal in cross-section (Martin, 1999). However, in mesungulatids, as well as in the basal meridiolestid *Leonardus*, the molariform roots are transversely expanded and mesiodistally compressed (Bonaparte, 1990; Rougier *et al.,* 2009a; 2009b; 2011; Chornogubsky, 2011). In *Necrolestes* the roots are also anteroposteriorly compressed and transversely expanded, occupying most of the buccolingual extension of the molar crowns (Asher *et al.,* 2007).

6. Meckelian groove absent (Character 4-2). In basal mammaliaforms, including basal Jurassic dryolestoids, a well-developed meckelian sulcus is present on the medial surface of dentary (Krebs, 1969; 1971; Martin, 1995; 1999; Kielan-Jaworowska *et al.,* 2004; Rich *et al.,* 2005). This sulcus is absent in Cretaceous dryolestoids, including *Crusafontia* and all Meridiolestida (e.g., *Cronopio*, *Coloniatherium*; Rougier *et al.,* 2009b; 2011). The absence of a meckelian groove is also reported in most living and extinct metatherian and eutherian mammals (with the exception of *Kokopellia*, *Prokennalestes*, *Eomaia,* and *Kielantherium*,

among others; Dashzeveg & Kielan-Jaworowska, 1984; Kielan-Jaworowska & Dashzeveg, 1989; Ji *et al.,* 2002; Kielan-Jaworowska *et al.,* 2004). In *Necrolestes* there is no sign of a meckelian sulcus on the dentary (Asher *et al.,* 2007) (Figs. 4, 5). In the present analysis, this character is recovered as a synapomorphy of the Meridiolestida, including *Necrolestes* (Appendix 3).

7. Three upper and lower molars (Character 127-1 in Rougier *et al.,* 2011). Basal dryolestoids are characterized by a large number of molariforms, usually more than 6 lower and upper molars (Martin, 1999). In contrast, in Meridiolestida (e.g., *Peligrotherium*, *Cronopio*, *Coloniatherium*; Rougier *et al.,* 2009b; 2011) only 3 molars are present in upper and lower dentitions. Patterson (1958) concluded that *Necrolestes* carried a number of 4 molars. However, recent analyses have modified such interpretation and recent authors agree that *Necrolestes* possessed only three upper and lower molars (Asher *et al.,* 2007; Goin *et al.,* 2007), a tooth count matching that of meridiolestidan dryolestoids.

Although present phylogenetic analysis places *Necrolestes* in a basal polytomy with other meridiolestidan taxa, this genus exhibits interesting similarities with *Cronopio.* They are: a two-rooted first premolar, a well-developed parastylar hook on the PM3, and single-rooted hypsodont-like molariforms (Asher *et al.,* 2007; Rougier *et al.,* 2011; Figs. 4, 5). These derived features are shared by these two Patagonia taxa, being absent in the remaining dryolestoids. However, in the context of the whole evidence, these features are not recovered as synapomorphic of a clade solely formed by *Cronopio* and *Necrolestes*.

In sum, the phylogenetic analysis here performed results in the inclusion of *Necrolestes* within the dryolestoid subclade Meridiolestida (Fig. 2). The consensus tree depicting such relationships is 2365 steps in length (Figs. 2, 3). In the context of our analysis, 54 additional steps are required to move *Necrolestes* as a basal metatherian, and 53 extra steps to move *Necrolestes* from Dryolestoidea to base of Theria.

Biogeographical implications

During Campanian-Maastrichtian times dryolestoids and gondwanatherians were present in southern South America (Bonaparte, 1986; 1993; 2002; Kielan-Jaworowska *et al.,* 2007; Gurovich & Beck, 2009; Rougier *et al.,* 2011), the first ones being currently represented by more than dozen species (Bonaparte, 2002; Rougier *et al.,* 2009a; 2009b; 2011). Dryolestoids were the numerically dominant and most diverse group of mammals by the end of the Cretaceous in Patagonia, and also probably other southern landmasses (Bonaparte, 2002). They radiated into sharp-toothed, small-sized insectivores such as *Cronopio* and *Leonardus*, as well as bulkier omnivorous-herbivorous forms, the mesungulatids. Mesungulatids evolved a highly derived dentition, which paralleled the morphology of basal condylarthran mammals (Bonaparte, 1990; Gelfo & Pascual, 2001; Rougier *et al.,* 2009a).

The Cenozoic radiation of South American mammals was traditionally viewed as exclusively composed by tribosphenidan clades (cf. Simpson, 1980). More recently, however, it became evident that some non-tribosphenic Mesozoic lineages survived in Patagonia and Antarctica up to the Eocene, including monotremes, gondwanatherians, and mesungulatid dryolestoids (Gelfo & Pascual, 2001; Goin *et al.,* 2006; Pascual & Ortíz-Jaureguizar, 2007; Rougier *et al.,* 2009a). Inclusion of *Necrolestes* within Meridiolestida dryolestoids indicates that the mammalian faunas from the Cenozoic of South America were not solely constituted by eutherians and metatherians as previously thought. Moreover, it is worth noting that the fossil record of *Necrolestes* is restricted to early-middle Miocene beds of Patagonia (Goin *et al.,* 2007). No remains of *Necrolestes*-like creatures have been reported so far from South American Cenozoic beds younger than early Miocene, thus suggesting that the *Necrolestes* lineage probably became extinct in the course of the Miocene epoch. Sister group relationships of *Necrolestes* with the Late Cretaceous meridiolestoid clade *Leonardus* + Mesungulatoidea supports the inference of a ghost lineage for more than 40 my, ranging from the Late Cretaceous to the Miocene epoch. This indicates that the history of the *Necrolestes*-lineage still stands to be unveiled, and that probably a large number of Cenozoic dryolestoids still remain to be discovered.

CONCLUSIONS

Asher *et al.* (2007) summarized the uncertainities on the taxonomic affinities of *Necrolestes* asking if this taxon is a marsupial, placental, or part of a "prototherian" radiation on the stem group leading to Theria. As noted by Asher *et al.* (2007), referral of *Necrolestes* to Metatheria constituted the less complicated biogeographic scenario, but not the best supported phylogenetic

hypothesis. Dryolestoid affinities for *Necrolestes* constitute the most parsimonious phylogenetic solution, and it is also paleobiogeographically congruent with the presence of derived dryolestoids in South America at the beginning of the Tertiary Period (Gelfo and Pascual, 2001).

The new systematic allocation of *Necrolestes* within Dryolestoidea considerably extends the biochron of this mammalian group, as well as expands the morphological disparity and ecological roles of dryolestoids, adding a fossorial mode of life to the adaptive repertoire of this mammalian clade.

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Appendix 1. Character list

Mandible

1. Post-dentary trough (behind the tooth row): (0) Present; (1) Absent. ***Necrolestes*: (1) Absent.**
2. Separate scars for the surangular/prearticular in the mandible: (0) Present; (1) Absent. ***Necrolestes*: (?) unknown.**
3. Overhanging medial ridge above the post-dentary trough (behind the tooth row): (0) Present; (1) Absent. ***Necrolestes*: (1) Absent.**
4. Degree of development of Meckel's sulcus: (0) Well developed; (1) Weakly developed; (2) Vestigial or absent. ***Necrolestes*: (2) Absent.**
5. Curvature of Meckel's sulcus (under the tooth row): (0) Parallel to the ventral border of the mandible; (1) Convergent on the ventral border of the mandible. ***Necrolestes*: (?) Not applicable.**
6. Groove for the replacement dental lamina (= Crompton's groove): (0) Present; (1) Absent. ***Necrolestes*: (1) Absent.**
7. Angular process of the dentary: (0) Weakly developed to absent; (1) Present, distinctive but not inflected; (2) Present and transversely flaring [This is different from character state (4) in having a lateral expansion of the angle and in lacking the anterior shelf]; (3) Present and slightly inflected; (4) Present, strongly inflected, and continuing anteriorly as the mandibular shelf. ***Necrolestes*: (1) Present, distinctive but not inflected.**
8. Position of the angular process of the dentary relative to the dentary condyle: (0) Anterior position (the angular process is below the main body of the coronoid process, separated widely from the dentary condyle); (1) Posterior position (the angular process is positioned at the level of the posterior end of the coronoid process, either close to, or directly under the dentary condyle). ***Necrolestes*: (0) anterior position.**
9. Vertical elevation of the angular process of the dentary relative to the molar alveoli: (0) Angular process low, at or near the level of the ventral border of the mandibular horizontal ramus; (1) Angular process high, at or near the level of the molar alveolar line (and far above the ventral border of the mandibular horizontal ramus). ***Necrolestes*: (0) low.**
10. Flat ventral surface of the mandibular angle: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
11. Exoflection of the angular process of mandible: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
12. Coronoid bone (or its attachment scar): (0) Present; (1) Absent. ***Necrolestes*: (1) Absent.**
13. Location of the mandibular foramen (posterior opening of the mandibular canal): (0) Within the postdentary trough or in the posterior part of Meckel's sulcus; (1) In the pterygoid fossa and offset from Meckel's sulcus (the intersection of Meckel's sulcus at the pterygoid margin is ventral and posterior to the foramen); (2) In the pterygoid fossa and in alignment with the posterior end of Meckel's sulcus; (3) In the pterygoid fossa but not associated with Meckel's sulcus; (4) Not associated with any of the above structures. ***Necrolestes*: (4) Not associated.**
14. Vertical position of the mandibular foramen: (0) Below the alveolar plane; (1) At or above the alveolar plane. ***Necrolestes*: (1) At or above the alveolar plane.**
15. Concavity (fossa) for the reflected lamina of the angular bone on the dentary angular process: (0) Present the medial side; (1) Present on the posterior aspect; (2) Absent. ***Necrolestes*: (2) Absent.**
16. Splenial bone as a separate element (as indicated by its scar on the dentary): (0) Present; (1) Absent ***Necrolestes*: (1) Absent.**
17. Relationship of the "postdentary" complex (surangular-articular-prearticular) to the craniomandibular joint (CMJ) [CMJ is made of several bones in the stem groups of mammals or mammaliaforms, whereas the temporomandibular joint (TMJ) is the medical and veterinary anatomical term applicable to living mammals in which the jaw hinge is made only of the temporal (squamosal) bone and the dentary. CMJ and TMJ are used interchangeably here as appropriate to the circumstances]: (0) Participating in CMJ; (1) Excluded from CMJ. ***Necrolestes*: (1) excluded.**
18. Contact of the surangular bone (or associated postdentary element) with the squamosal: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
19. Pterygoid muscle fossa on the medial side of the ramus of the mandible: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**
20. Medial pterygoid ridge (shelf) along the ventral border of the ramus of the mandible: (0) Absent; (1) Present; (2) Pterygoid shelf present and reaching the dentary condyle via a low crest. ***Necrolestes*: (0) Absent.**
21. Ventral border of the masseteric fossa: (0) Absent; (1) Present as a low and broad crest; (2) Present as a well-defined and thin crest. ***Necrolestes*: (1) low and broad.**
22. Crest of the masseteric fossa along the anterior border of the coronoid process: (0) Absent or weakly developed; (1) Present and distinctive; (2) Hypertrophied and laterally flaring. ***Necrolestes*: (1) present and distinctive.**
23. Anteroventral extension of the masseteric fossa: (0) Absent; (1) Extending anteriorly onto the body of the mandible; (2) Further anterior extension below the ultimate premolar. ***Necrolestes*: (0) Absent.**
24. Labial mandibular foramen inside the masseteric fossa: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
25. Posterior vertical shelf of the masseteric fossa connected to the dentary condyle: (0) Absent; (1) Present as a thin crest along the angular margin of mandible; (2) Present as a thick, vertical crest. ***Necrolestes*: (1) Present.**
26. Posterior-most mental foramen: (0) In the canine and anterior premolar (premolariform) region (in the saddle behind the canine eminence of the mandible); (1) Below the penultimate premolar (under the anterior end of the functional postca-

nine row); (2) Below the ultimate premolar; (3) At the ultimate premolar and the first molar junction; (4) Under the first molar. ***Necrolestes*: (0) in the canine and anterior premolar region. Comments.** Luo *et al.* (2007) codify this character as (1) for *Dryolestes*. On the contrary, Rougier *et al.* (2011) codify it as (0). Martin (1999) clearly illustrate several mandibles of *Dryolestes* indicating that the posterior-mental foramen is located at the anterior premolar region (below the first or second lower premolars), far from the penultimate premolar. In this way, it is coded here as (0), following Rougier *et al.* (2011).

27. Articulation of the dentary and the squamosal: (0) Absent; (1) Present, but without condyle/glenoid; (2) Present, but with condyle/glenoid. ***Necrolestes*: (2) Present with condyle/glenoid.**
28. Shape and relative size of the dentary articulation: (0) Condyle small or absent; (1) Condyle massive, bulbous, and transversely broad in its dorsal aspect; (2) Condyle mediolaterally narrow and vertically deep, forming a broad arc in lateral outline, either ovoid or triangular in posterior view. ***Necrolestes*: (1) Condyle massive and transversely broad in dorsal aspect.**
29. Orientation of the dentary peduncle (condylar process) and condyle: (0) Dentary peduncle more posteriorly directed; (1) Dentary condyle continuous with the semicircular posterior margin of the dentary; the condyle is facing up due to the upturning of the posterior-most part of the dentary; (2) Dentary articulation extending vertically for the entire depth of the posterior manidbular ramus; it is confluent with the ramus and without a peduncle; the dentary articulation is posteriorly directed; (3) More vertically directed dentary peduncle. ***Necrolestes*: (1) Dentary continuous**
30. Ventral (inferior) border of the dentary peduncle: (0) Posteriorly tapering; (1) Columnar and with a lateral ridge; (2) Ventrally flaring; (3) Robust and short; (4) Ventral part of the peduncle and condyle continuous with the ventral border of the mandible. ***Necrolestes*: (3) robust and short.**
31. Gracile and elongate dentary peduncle: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**
32. Position of the dentary condyle relative to the level of the postcanine alveoli: (0) Below or about the same level; (1) Above. ***Necrolestes*: (1) Above. *Peligrotherium*: (1) Above.**
33. Tilting of the coronoid process of the dentary (measured as the angle between the anterior border of the coronoid process and the horizontal alveolar line of all molars): (0) Coronoid process strongly reclined and the coronoid angle obtuse (≥150º); (1) Coronoid process less reclined (135º-145º); (2) Coronoid process less than vertical (110º-125º); (3) Coronoid process near vertical (95º to 105º). ***Necrolestes*: (2) 110º-125º.**
34. Gracile base of the coronoid process: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
35. Height of the coronoid process of the dentary: (0) Not reduced; (1) reduced. ***Necrolestes*: (0) Not reduced.**
36. Alignment of the ultimate molar (or posteriormost postcanine) to the anterior margin of the dentary coronoid process (and near the coronoid scar if present): (0) Ultimate molar medial to the coronoid process; (1) Ultimate molar aligned with the coronoid process. ***Necrolestes*: (0) ultimate molar medial to the coronoid process.**
37. Direction of lower jaw movement during occlusion (as inferred from teeth) (character 115 de Rougier *et al.*, 2011): (0) Dorsal movement; (1) Dorsomedial movement with a significant medial component; (2) Dorsoposterior movement. ***Necrolestes*: (1) dorsomedial movement with a significant medial component.**
38. Dentary symphysis: (0) Fused; (1) Unfused. ***Necrolestes*: (1) Unfused.**
39. Rostral mandibular spout: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**

Premolars

40. Ultimate upper premolar - metastylar lobe: (0) Reduced or absent; (1) Enlarged and wing-like. ***Necrolestes*: (0) Reduced.**
41. Ultimate upper premolar - metacone or metaconal swelling: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
42. Ultimate upper premolar - protocone or protoconal swelling: (0) Little or no lingual swelling; (1) Present. ***Necrolestes*: (0) No lingual swelling.**
43. Penultimate upper premolar - protocone or protoconal swelling: (0) Little or no lingual swelling; (1) Protoconal swelling; (2) Distinctive and functional protocone. ***Necrolestes*: (0) No lingual swelling.**
44. Position of the tallest posterior upper premolar within the premolar series: (0) No premolar standing out; (1) In ultimate premolar position; (2) In penultimate premolar position. ***Necrolestes*: (0) No premolar standing out.**
45. Diastema posterior to the first upper premolar (applicable to taxa with premolar molar differentiation): (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
46. Ultimate lower premolar - symmetry of the main cusp a (= protoconid): (0) Asymmetrical (anterior edge of cusp a is more convex in outline than the posterior edge); (1) Symmetrical (anterior and posterior cutting edges are equal or subequal in length; neither edge is more convex or concave than the other in lateral profile). ***Necrolestes*: (0) Asymmetrical.**
47. Ultimate lower premolar - anterior cusp b (= paraconid): (0) Absent or indistinctive; (1) Present and distinctive; (2) Enlarged. ***Necrolestes*: (1) Present and distinctive.**
48. Ultimate lower premolar - arrangement of principal cusp a, cusp b (if present), and cusp c (assuming the cusp to be c if there is only one cusp behind the main cusp a): (0) Aligned in a single straight line or at a slight angle; (1) Distinctive triangulation; (2) Premolar multicuspate in longitudinal row(s).

***Necrolestes*: (1) triangulation.**

49. Ultimate lower premolar - posterior (distal) cingulid or cingular cuspule (in addition to cusp c or the metaconid if the latter cusp is present on a triangulated trigonid). (0) Absent or indistinctive; (1) Present; (2) Present, in addition to cusp c or the c swelling; (3) Presence of the continuous posterior (distal) cingulid at the base of the crown. ***Necrolestes*: (0) Absent.**
50. Ultimate lower premolar - outline: (0) Laterally compressed (or slightly angled); (1) Transversely wide (by trigonid); (2) Transversely wide (by talonid). ***Necrolestes*: (1) Transversely wide (by trigonid).**
51. Ultimate lower premolar - labial cingulid: (0) Absent or vestigial; (1) Present (at least along the length of more than half of the crown). ***Necrolestes*: (0) Absent.**
52. Ultimate lower premolar - lingual cingulid: (0) Absent or vestigial; (1) Present. ***Necrolestes*: (0) Absent.**
53. Ultimate lower premolar - relative height of primary cusp a to cusp c (measured as the height ratio of a and c from the bottom of the valley between the two adjacent cusps): (0) Indistinctive; (1) Posterior cusp c distinctive but less than 30% of the primary cusp a; (2) Posterior cusp c and primary cusp a equal or subequal in height (c is 40%-100% of a). ***Necrolestes*: (2) Posterior cusp c and primary cusp a equal or subequal in height.**
54. Penultimate lower premolar - paraconid (=cusp b): (0) Absent; (1) Present but not distinctive; (2) Distinctive and slightly enlarged. ***Necrolestes*: (2) Distinctive and slightly enlarged.**
55. Penultimate lower premolar - arrangement of principal cusp a, cusp b (if present), and cusp c (we assume the cusp to be c if there is only one cusp behind the main cusp a): (0) Cusps in straight alignment (for a tooth with a single cusp, the anterior and posterior crests from the main cusp are in alignment); (1) Cusps in reversed triangulation; (2) With multicusps in longitudinal row(s). ***Necrolestes*: (0) cusps in alignment.**
56. Elongation of posterior premolars: (0) Absent; (1) Present. ***Necrolestes*: (0) absent.**

Molar Morphology

57. Alignment of the main cusps of the anterior lower molar(s) (justification for separating this feature from the next character on the list): Several taxa of "obtuse-angled symmetrodonts" and eutriconodont amphilestids show a gradient of variation in cusp-triangulation along the molar series; the degree of triangulation may be different between the anterior and posterior molars). (0) Single longitudinal row; (1) Reversed triangle-acute (≤90º); (2) Multiple longitudinal multicuspate rows. ***Necrolestes*: (1) Reversed triangle.**
58. Triangulation of cusps in the posterior molars: (0) Absent; (1) Multi-row and multi-cuspate; (2) Posterior molars slightly triangulated; (3) Posterior molars fully triangulated. ***Necrolestes*: (3) Posterior molar fully triangulated.**
59. B1 cusp on the upper molar (applicable to molars with triangulation): (0) Absent; (1) Present: ***Necrolestes*: (0) Absent.**
60. Postvallum/prevallid shearing (angle of the main trigonid shear facets, based on the second lower molar): (0) Absent; (1) Present, weakly developed, slightly oblique; (2) Present, strongly developed and more transverse; (3) Present, strongly developed, short and slightly oblique. ***Necrolestes*: (2) Present, strongly developed and transverse.**
61. Rank of postvallum shear (on the upper second molar; applicable to molars with reversed triangulation of cusps) (increasing the ranks of postvallum shear and can be ordered): (0) Present but only by the first rank: postmetacrista; (1) Present, with the addition of a second rank (postprotocrista below postmetacrista) but the second rank does not reach labially below the base of the metacone; (2) Metacingulum/metaconule present, in addition to postprotocrista, but the metacingulum crest does not extend beyond the base of the metacone; (3) Metacingulum extended beyond metacone; (4) Metacingulum extended to the metastylar lobe; (5) Second rank postvallum shear forming a broad shelf (as in selenodonty). ***Necrolestes*: (0) Postmetacrista.**
62. Postcingulum: (0) Absent or weak; (1) Present; (2) Present and reaching past the metaconule; (3) Formed by the hypoconal shelf raised to near the level of the protocone. ***Necrolestes*: (0) absent.**
63. Precise opposition of the upper and lower molars: (0) Absent; (1) Present (either one-to-one, or occluding at the opposite embrasure or talonid); (2) Present (one lower molar contacts sequentially more than one upper molar). ***Necrolestes*: (1) Present.**
64. Relationships between the cusps of the opposing upper and lower molars: (0) Absent; (1) Present, lower primary cusp a occludes in the groove between upper cusps A, B; (2) Present, lower main cusp a occludes in front of the upper cusp B and into the embrasure between the opposite upper tooth and the preceding upper tooth; (3) Present, parts of the talonid occluding with the lingual face (or any part) of the upper molar; (4) Lower multicuspate rows alternately occluding between the upper multicuspate rows; (5) Columnar tooth without cusps and with beveled wear across theentire crown contact surface. ***Necrolestes*: (2) lower cusp a occluding the embrasure of upper molars.**
65. Protoconid (cusp a) and metaconid (cusp c) height ratio (on the lower second molar): (0) Protoconid distinctively higher; (1) Protoconid and metaconid nearly equal in height. ***Necrolestes*: (1) Protoconid and metaconid nearly equal in height.**
66. Relative height and size of the base of the paraconid (cusp b) and metaconid (cusp c) (on the lower second molar): (0) Paraconid distinctively higher than the metaconid; (1) Paraconid and metaconid nearly equal in height; (2) Paraconid lower than metaconid; (3) Paraconid reduced or absent.

***Necrolestes*: (1) Paraconid and metaconid nearly equal in height.**

67. Elevation of the cingulid base of the paraconid (cusp b) relative to the cingulid base of the metaconid (cusp c) on the lower molars: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
68. Cristid obliqua: (0) Absent; (1) Present, contact closest to the middle posterior of the metaconid; (2) Present, contact closest to the lowest point of the protocristid; (3) Present, contact closest to the middle posterior of the protoconid. ***Necrolestes*: (0) Absent.**
69. Lower molar - medial and longitudinal crest (='pre-entocristid' or 'pre-hypoconulid') on the talonid heel (only applicable to taxa with talonid or at least a cusp d): (0) Talonid (or cusp d) has no medial and longitudinal crest; (1) Medial-most cristid ('pre-entoconid cristid') of the talonid in alignment with the metaconid or with the postmetacristid if the latter is present (the postmetacristid is defined as the posterior crest of metaconid that is parallel to the lingual border of the crown), but widely separated from the latter; (2) Medial-most cristid of the talonid is hypertrophied and in alignment with the postmetacristid and abuts the latter by a V-notch; (3) 'Pre-entocristid' crest is offset from the metaconid (and postmetacristid if present), and the 'pre-entocristid' extending anterolingually past the base of the metaconid. ***Necrolestes*: (?) Not applicable.**
70. Posterior lingual cingulid of the lower molars: (0) Absent or weak; (1) Distinctive; (2) Strongly developed, crenulated with distinctive cuspules (such as the kuhneocone). ***Necrolestes*: (0) Absent or weak.**
71. Anterior internal (mesio-lingual) cingular cuspule (e) on the lower molars: (0) Present as an anterior cuspule but not at the cingulid level; (1) Present, at the cingulid level; (2) Present, positioned above the cingulid level; (3) hypertrophied cusp e = pseudo-hypoconulid; (4) Absent. ***Necrolestes*: (4) absent.**
72. Anterior and labial (mesio-buccal) cingular cuspule (f): (0) Absent; (1) Present; (2) Hypertrophied to form pseudo-hypoconid. ***Necrolestes*: (0) Absent.**
73. Mesial cingulid features above the gum: (0) Absent; (1) Weak and discontinuous, with individualized cuspules below the trigonid (as individual cuspule e, f, or both, but e and f are not connected); (2) Present, in a continuous shelf below the trigonid (with no relations to the protoconid and paraconid), without occlusal function; (3) Present, with occlusal contact to the upper molar. ***Necrolestes*: (0) absent.**
74. Cingulid shelf wrapping around the anterolingual corner of the molar to extend to the lingual side of the trigonid below the paraconid: (0) Absent; (1) Present, without occlusal function to the upper molars; (2) Present, with occlusal function to the upper molars. ***Necrolestes*: (0) Absent.**
75. Postcingulid (distal transverse cingulid above the gum level) on the lower molars: (0) Absent; (1) Present, horizontal above the gum level. ***Necrolestes*: (0) Absent.**
76. Interlocking mechanism between two adjacent lower molars: (0) Absent; (1) Present, posterior cingular cuspule d (or the base of the hypoconulid) of the preceding molar fits in between cingular cuspules e and f of the succeeding molar; (2) Present, posterior cingular cuspule d fits between cingular cuspule e and cusp b of the succeeding molar; (3) Present, posterior cingular cuspule d of the preceding molar fits into an embayment or vertical groove of the anterior aspect of cusp b of the succeeding molar (without any involvement of distinctive cingular cuspules in interlocking). (4) Anterior corner of succeeding lower molar overlapping posterior corner of preceding lower molar. ***Necrolestes*: (0) absent.**
77. Size ratio of the last three lower molars: (0) Ultimate molar is smaller than the penultimate molar ($m1 \geq m2 \geq m3$; or $m2 \geq m3 \geq m4$; or $m3 \geq m4 \geq m5$; or $m4 \geq m5 \geq m6$); (1) Penultimate molar is the largest of the molars ($m1 \leq m2 \leq m3 \geq m4$; or $m1 \leq m2 > m3$); (2) Ultimate molar is larger than the penultimate molar ($m1 \leq m2 \leq m3$); (3) Equal size. ***Necrolestes*: (0) Posteriorly enlarging gradient.**
78. Paraconid position relative to the other cusps of the trigonid on the lower molars (based on the lower second molar): (0) Paraconid in anterolingual position; (1) Paraconid lingually positioned (within lingual 1/4 of the trigonid width); (2) Paraconid lingually positioned and appressed to the metaconid; (3) Paraconid reduced in the selenodont/lophodont patterns. ***Necrolestes*: (0) Paraconid in anterolingual position.**
79. Orientation of the paracristid (or the crest between cusps a and b) relative to the longitudinal axis of the molar: (0) Longitudinal orientation; (1) Oblique; (2) Nearly transverse. ***Necrolestes*: (2) Nearly transverse.**
80. Angle of the paracristid (b-a crest) and the protocristid (a-c crest) on the lower molar: (0) > 90º; (1) 90º ~ 50º; (2) < 35º. ***Necrolestes*: (2).**
81. Mesiolingual vertical crest of the paraconid on the lower molars (applicable only to taxa with reversed triangulation of the molar cusps): (0) Rounded; (1) Forming a keel. ***Necrolestes*: (0) rounded.**
82. Anteroposterior shortening at the base of the trigonid relative to the talonid (applicable only to taxa with a talonid heel with a distal cusp d; measured at the lingual base of the lower second molar trigonid where possible): (0) Trigonid long (extending over 3/4 of the tooth length); (1) Swelling on the side walls of the trigonid (taxa assigned to this character state have a trigonid length ratio 45%~50%; but their morphology is different from all other states in that their side walls are convex); (2) No shortening (trigonid 50-65% of tooth length); (3) Some shortening (the base of trigonid < 50% of tooth length); (4) Anteroposterior compression of trigonid (trigonid 40~45% of the tooth length). ***Necrolestes*: (0) trigonid long.**
83. Molar (the lower second molar measured where

possible) trigonid/talonid heel width ratio: (0) Narrow (talonid ≤40% of trigonid); (1) Wide (talonid is 40-70% of the trigonid in width); (2) Talonid is equal or wider than trigonid. ***Necrolestes*: (?) not applicable.**

84. Lower molar hypoflexid (concavity anterolabial to the hypconid or cusp d): (0) Absent or shallow (all "triconodont-like" teeth are coded as "0" here as long as they have cuspule d); (1) Deep (40~50% of talonid width); (2) Very Deep (>65%); (3) Pseudohypoflexid (40% to 65% of the pseudo-talonid width). ***Necrolestes*: (0) Absent.**
85. Morphology of the talonid (or the posterior heel) of the molar: (0) Absent; (1) Present, as an incipient heel, a cingulid, or cingular cuspule (d); (2) Present, as a transverse 'V-shaped' basin with two functional cusps; (3) Present, as an obtuse 'V-shaped' triangle; (4) Present, as a functional basin, rimmed with 3 functional cusps (if the entoconid is vestigial, there is a functional crest to define the medial rim of the basin). ***Necrolestes*: (0) Absent.**
86. Hypoconid (we designate the distal cingulid cuspule d as the homolog to the hypoconid in the teeth with linear alignment of the main cusps; we assume the cusp to be the hypoconid if there is only a single cusp on the talonid in the teeth with reversed triangulation): (0) Present, but not elevated above the cingulid level; (1) Present (as distal cusp d, *sensu* Crompton 1971), elevated above the cingulid level, labially positioned (or tilted in thelingual direction); (2) Present (larger than cusp d, with occlusal contact to the upper molar), elevated above the cingulid level, labially positioned. ***Necrolestes*: (?), not applicable.**
87. Hypoconulid: (0) Absent; (1) Present, and median (near the mid-point of the transverse talonid width); (2) Present, and placed within the lingual 1/3 of the talonid basin; (3) Incorporated into the crest of lophodont or selenodont conditions. ***Necrolestes*: (0) Absent.**
88. Anterior lower molar (preferably the first, or the second if the first is not available) - hypoconulid - anteroposterior orientation: procumbent vs. reclined (applicable to the taxa with at least two cusps on the talonid): (0) Cusp tip reclined and the posterior wall of the hypoconulid is slanted and overhanging the root; (1) Cusp tip procumbent and the posterior wall of the cusp is vertical; (2) Cusp tip procumbent and the posterior wall is gibbous. ***Necrolestes*: (?) not applicable.**
89. Hypoconulid labial postcingulid (shelf) on the lower molars: (0) Absent; (1) Present as a crest descending mesiolabially from the apex of the hypoconulid to the base of the hypoconid. ***Necrolestes*: (0) absent.**
90. Last lower molar - hypoconulid - orientation and relative size: (0) Short and erect; (1) Tall (higher than hypoconid) and recurved. ***Necrolestes*: (?) Not applicable.**
91. Entoconid: (0) Absent; (1) Present, about equal distance to the hypoconulid as to the hypoconid; (2) Present, with slight approximation to the hypoconulid (distance between the hypoconulid and entoconid noticeably shorter than between the hypoconulid and hypoconid); (3) Present, and twinned with the hypoconulid. ***Necrolestes*: (0) Absent.**
92. Height ratio of the medial side of the crown (apex of the hypoconid to the base of the labial crown) vs. the most lingual cusp on the talonid to the base of the labial crown (this character can be based either on the entoconid if the entoconid is present or the hypoconulid if the entoconid cannot be scored): (0) Entoconid absent on the talonid heel; (1) Entoconid lower than the hypoconid; (2) Entoconid near the height of the hypoconid; (3) Entoconid near the height of the hypoconid and linked to the hypoconid by a transverse crest. ***Necrolestes*: (?) Not applicable.**
93. Alignment of the paraconid, metaconid, and entoconid on the lower molars (applicable only to taxa with triangulation of the trigonid cusps and the entoconid present on the talonid): (0) Cusps not aligned; (1) Cusps aligned. ***Necrolestes*: (?) Not applicable.**
94. The length vs. width ratio of the functional talonid basin of the lower molars (in occlusal view, measured at the cingulid level, and based on the second molar): (0) Longer than wide (or narrows posteriorly); (1) Length equals width; (2) Wider than long. ***Necrolestes*: (?) Not applicable.**
95. Elevation of the talonid (measured as the height of the hypoconid from the cingulid on the labial side of the crown) relative to the trigonid (measured as the height of protoconid from the cingulid) (applicable only to the teeth with reversed triangulation): (0) Hypoconid/protoconid height ratio less than 20% (hypoconid or cusp d is on the cingulid); (1) Hypoconid/protoconid height ratio between 25% and 35% (talonid cusp elevated above the cingulid level); (2) Hypoconid/protoconid height ratio between 40% and 60%; (3) Hypoconid/protoconid height ratio between >60% and 80%; (4) Equal height. ***Necrolestes*: (?) Not applicable.**
96. Size (labiolingual width) of the upper molar labial stylar shelf on the penultimate molar: (0) Absent; (1) Present and narrow; (2) Present and broad. ***Necrolestes*: (2) Present and broad.**
97. Presence vs. absence of the ectoflexus on the upper second molar (or postcanines in the middle portion of the postcanine row). (0) Absent or weakly developed; (1) Present. ***Necrolestes*: (0) absent.**
98. Ectoflexus gradient along the molar series (see the above for justification of separating presence/absence from the gradient of the ectoflexus on the upper molar(s)): (0) Present on penultimate molar, but weakly developed or absent on the anterior molars; (1) Present on the penultimate and preceding molars. ***Necrolestes*: (?) not applicable.**
99. Morphological features on the labial cingulum or stylar shelf of the upper molars (excluding the parastyle and metastyle): (0) Indistinctive; (1) Distinctive cingulum, without cuspules; (2) Individualized or even hypertrophied cuspules; (3) W-pattern on stylar shelf; (4) Cingulum crenulated

with distinctive and even-sized multiple cuspules. ***Necrolestes*: (0) indistinctive.**

100. Upper molar protocone: (0) Functional cusp and lingual swelling absent; (1) Functional cusp absent, but the lingual side is more swollen than the labial side at the cingular level; (2) Functional cusp present. ***Necrolestes*: (0) functional cusp absent.**
101. Degree of labial shift of the protocone (distance from the protocone apex to the lingual border vs. the total tooth width, in %) (applicable only to those taxa with reversed triangulation): (0) Protocone present but no labial shift (10%-20%); (1) Moderate labial shift (25%-30%); (2) Substantial labial shift (≥ 40%). ***Necrolestes*: (?) not applicable.**
102. Morphology of the protocone (applicable only to those taxa with reversed triangulation and a lingual swelling of the upper molar): (0) Protoconal region present but no distinct protocone; (1) Protocone present, its apical portion anteroposteriorly compressed; (2) Apical portion slightly expanded; (3) Apical portion expanded; (4) Apical portion forming an obtuse triangle with the protoconal cristae. ***Necrolestes*: (?) Not applicable.**
103. Height of the protocone relative to the paracone and metacone (whichever is highest of the latter two): (0) Protocone markedly lower (less than 70%); (1) Protocone of intermediate height (70%~80%); (2) Protocone near the height of paracone and metacone (within 80%). ***Necrolestes*: (?) not applicable.**
104. Height and size of the paracone (cusp B) and metacone (cusp C) (based on the upper second molar if available): (0) Paracone noticeably higher and larger at the base than metacone; (1) Paracone slightly larger than metacone; (2) Paracone and metacone of equal size or paracone lower than metacone; (3) metacone absent (taken from Bonaparte, 1990). ***Necrolestes*: (3) Absent.**
105. Metacone position relative to paracone: (0) Metacone labial to paracone; (1) Metacone about the same level as paracone; (2) Metacone lingual to paracone. ***Necrolestes*: (?) not applicable.**
106. Base of the paracone and metacone (based on the upper second molar if available, applicable only to triangulated molars): (0) Merged; (1) Separated. ***Necrolestes*: (?) not applicable.**
107. Centrocrista between the paracone and the metacone of the upper molars (applicable only to taxa with well-developed metacone and distinctive wear facets 3 and 4): (0) Straight; (1) V-shaped, with labially directed postparacrista and premetacrista. ***Necrolestes*: (?) not applicable.**
108. Anteroposterior width of the conular region (with or without conules) on the upper molars: (0) Narrow (anteroposterior distance medial to the paracone and metacone less than 0.30 of total tooth length); (1) Moderate development (distance between position of conules = 0.31—0.50 of total tooth length); (2) Wide (distance between conules greater than 0.51 of total tooth length); (3) Expanded. ***Necrolestes*: (?) Not applicable.**
109. Presence of the paraconule and metaconule on the upper molars: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
110. Relative position of the paraconule and metaconule on the upper first and second molars: (0) Paraconule and metaconule closer to the protocone; (1) Both positioned near the midpoint of the protocone-metacone; (2) Paraconule and metaconule labial to the midpoint. ***Necrolestes*: (?) Not applicable.**
111. Internal conular cristae (conular wing): (0) Cristae indistinctive; (1) Cristae distinctive and wing-like. ***Necrolestes*: (?) Not applicable.**
112. Parastylar groove (on upper second molar): (0) Weak or absent; (1) Moderately to well developed. ***Necrolestes*: (0) Absent.**
113. Stylar cuspule "A", the parastyle, on the upper molars (of the Bensley-Simpson system; cuspule "E" of the Crompton designation): (0) Present (at least a swelling is present); (1) Absent. ***Necrolestes*: (1) Absent.**
114. Preparastyle on the upper first molar (applicable to molars with triangulation): (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
115. Stylar cuspule "B" (opposite the paracone) (based on the upper second molar if available): (0) Vestigial to absent; (1) Small but distinctive; (2) Subequal to the parastyle; (3) Large (subequal to parastyle), with an extra "B-1" cuspule in addition to "B". ***Necrolestes*: (1) Small but distinctive.**
116. Stylar cuspule "C" (near the ectoflexus) on the penultimate upper molar: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
117. Stylar cuspule "D" (opposite the metacone) on the penultimate upper molar: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
118. Absence vs. presence and size of the stylar cuspule "E" (Bensley-Simpson designation; not the Crompton cusp E): (0) Absent or poorly developed; (1) Present, less developed than or subequal to stylar cuspule "D"; (2) Present and better developed than cuspule "D". ***Necrolestes*: (0) Absent.**
119. Position of the stylar cuspule "E" relative to cusp "D" or "D-position": (0) "E" more lingual to "D" or "D-position"; (1) "E" distal to or at same level as "D" or "D-position". ***Necrolestes*: (?) Not applicable.**
120. Upper molar interlock: (0) Absent; (1) Tongue-in-groove interlock; (2) Parastylar lobe of a succeeding molar lumbricated with the metastylar region of a preceding molar. ***Necrolestes*: (0) Absent.**
121. Size and labial extent of the metastylar lobe and parastylar lobe (based on the upper first molar if available; if not, then based on upper second): (0) Metastylar lobe smaller than the parastylar lobe; (1) Metastylar lobe of similar size and labial extent to the parastylar lobe; (2) Metastylar lobe much larger than the parastylar lobe; (3) Metastylar lobe absent. ***Necrolestes*: (2) Metastylar lobe much larger.**
122. Salient postmetacrista on the upper molars (applicable to taxa with reversed triangulation): (0) Absent or weakly developed; (1) Well-developed but no longer than the metacone-protocone distance;

(2) Hypertrophied and longer than the metacone-protocone distance. ***Necrolestes*: (0) Absent.**

123. Selenodont molar pattern: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**

124. Outline of the lower first molar crown (in crown view): (0) Laterally compressed; (1) Oblong with slight labial bulge; (2) Triangular or tear-drop shaped; (3) Rectangular (or rhomboidal); (4) circular. ***Necrolestes*: (2) Triangular or tear-drop shaped.**

125. Aspect ratio and outline of the upper first molar: (0) Laterally compressed; (1) Longer than transversely wide (oval-shaped or spindle shaped); (2) Transversely wider than long (triangular outline); (3) Rectangular or nearly so; (4) circular. ***Necrolestes*: (2) transversely wider than long.**

126. Carnassial shearing blades on last upper premolar and first lower molar: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**

Molar Wear Pattern

127. Functional development of occlusal facets on individual molar cusps: (0) Absent; (1) Absent at eruption but developed later by crown wear; (2) Wear facets match upon tooth eruption (inferred from the flat contact surface upon eruption). ***Necrolestes*: (2).**

128. Topographic relationships of wear facets to the main cusps: (0) Wear pattern across the entire crown; (1) Lower cusps a, c support two different wear facets (facets 1 and 4) that contact the upper primary cusp A; (2) Lower cusps a, c support a single wear facet (facet 4) that contacts the upper primary cusp B (this facet extends onto cusp A as wear continues, but 1 and 4 do not develop simultaneous in these taxa); (3) Multicuspate series, each cusp may support 2 wear facets. ***Necrolestes*: (2) two cusps supporting a single facet.**

129. Development and orientation of prevallum/postvallid shearing (based on either upper or the lower molar structures): (0) Absent; (1) Present and obtuse; (2) Present, hypertrophied and transverse. ***Necrolestes*: (2) Present, hypertrophied and transverse.**

130. Wear facet 1 (a single facet supported by cusp a and cusp c) and facet 2 (a single facet supported by cusp a and cusp b): (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**

131. Upper molars - development of facet 1 and the preprotocrista (applicable to molars with reversed triangulation): (0) Facet 1 (prevallum crest) short, not extending to the stylocone area; (1) Facet 1 extending into the hook-like area near the stylocone; (2) Preprotocrista long, extending labially beyond the paracone. ***Necrolestes*: (0).**

132. Differentiation of wear facet 3 and facet 4 (applicable to taxa with a distal cusp d or "hypoconulid"): (0) Absent; (1) Present; (2) Facets 3 and 4 hypertrophied on the flanks of the strongly V-shaped talonid. ***Necrolestes*: (0) Absent.**

133. Orientation of facet 4 (on the posterior aspect of the hypoconid): (0) Present and oblique to the long axis of the tooth; (1) Present and forming a more transverse angle to the long axis of the tooth. ***Necrolestes*: (?) Not applicable.**

134. Morphology of the posterolateral aspect of the talonid (the labial face of the hypoconid or equivalent area of Crompton facet 4, applicable to taxa with fully basined talonid): (0) Gently rounded; (1) Angular. ***Necrolestes*: (?) Not applicable.**

135. Wear pattern within the talonid basin (applicable to those taxa with triangulated molars): (0) Absent; (1) Present; (2) Present apically on the crests of the talonid; (3) Apical wear on crest and lophodont. ***Necrolestes*: (0) absent.**

136. Development of the distal metacristid (applicable only to taxa with reversed triangulation): (0) Present; (1) Absent. ***Necrolestes*: (1) Absent.**

137. Differentiation of wear facets 5 and 6 on the labial face of the entoconid: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**

138. Surficial features on the occluding surfaces on the talonid (only applicable to taxa with reversed triangulation): (0) Smooth surface on the talonid heel (or on cusp d); (1) Multiple ridges within the talonid basin; (2) Talonid present, but wear occurs apically on the crests of cristid obliqua and hypoconid cristid (V-shaped talonid crests). ***Necrolestes*: (?) not applicable.**

139. Molar wear facets pseudo-3 and pseudo-4: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**

140. Molar wear facets pseudo-5 and pseudo-6: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**

141. Pseudo cusp e and f hypertrophied: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**

Other Dental Features

142. Number of lower incisors: (0) Five or more; (1) Four; (2) Three; (3) Two; (4) One; (5) No incisors. ***Necrolestes*: (1) Four.**

143. Number of upper incisors: (0) Five; (1) Four; (2) Three; (3) Two or one; (4) No incisors. ***Necrolestes*: (0) five.**

144. Lower anterior-most incisor enamel: (0) Covers the whole incisor; (1) Restricted anteriorly. ***Necrolestes*: (0).**

145. Lower anterior-most incisor with open root: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**

146. Upper anterior-most incisor enamel: (0) Covers the whole incisor; (1) Restricted anteriorly. ***Necrolestes*: (0).**

147. Upper anterior-most incisor with open root: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**

148. Upper canine - presence vs. absence, and size: (0) Present and enlarged; (1) Present and small; (2) Absent. ***Necrolestes*: (0) Present and enlarged.**

149. Number of upper canine roots: (0) One; (1) Two. ***Necrolestes*: (1) two.**

150. Lower canine - presence vs. absence and size: (0) Present and enlarged; (1) Present and small; (2) Absent. ***Necrolestes*: (0) Present and enlarged.**

151. Number of lower canine roots: (0) One; (1) Two. ***Necrolestes*: (1) Two.**
152. Number of upper premolars (only applicable to taxa with premolar vs. molar differentiation): (0) Five or more; (1) Four; (2) Three; (3) Two or less. ***Necrolestes*: (2) Three.**
153. Number of lower premolars: (0) Five or more; (1) Four; (2) Three; (3) Two or less. ***Necrolestes*: (2) Three.**
154. Number of lower molars or molariform postcanines: (0) Six or more; (1) Five; (2) Four; (3) Three; (4) Two or less. ***Necrolestes*: (3) Three.**
155. Number of upper molars or molariform postcanines (applicable only to those taxa that do not have multiple dental replacements): (0) Six or more; (1) Five; (2) Four; (3) Three; (4) Two or less. ***Necrolestes*: (3) three.**
156. Total number of upper postcanine loci: (0) More than 8 (including the loci plus the alveoli of shed anterior postcanines); (1) Eight; (2) Seven, (3) Six; (4) Five or less. ***Necrolestes*: (3) Six.**
157. Number of lower postcanine loci: (0) Eight or more; (1) Seven; (2) Six; (3) Five or less. ***Necrolestes*: (2) Six.**
158. Procumbency and diastema of first (functional) upper premolar or postcanine in relation to the upper canine: (0) Not procumbent and without diastema; (1) Procumbent and with diastema. ***Necrolestes*: (0) not procumbent and without diastema.**
159. Diastema separating the lower first and second premolars (defined as the first and second functioning premolar or premolariform postcanine): (0) Absent (gap less than one tooth root for whichever is smaller of the adjacent teeth); (1) Present, subequal to one tooth-root diameter or more; (2) Present, equal to or more than one-tooth length. ***Necrolestes*: (1) Present.**
160. Ultimate premolar bladed or crenulated: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
161. Upper anterior-most incisor: (0) Subequal to the remaining incisors, no diastema with the second incisor; (1) Anteriorly projecting, separated from the second incisor by a diastema; (2) Absent (as evidenced by a median gap between the mesial-most incisors). ***Necrolestes*: (0).**
162. Ultimate and penultimate upper incisors are relatively compressed laterally: (0) Absent; (1) Present, and spoon-shaped to rhomboid-shaped in lateral view; (2) Present, and spatulate in lateral view; (3) Ultimate and/or penultimate upper incisors bicuspate or tricuspate. ***Necrolestes*: (1).**
163. Staggered lower incisor (Hershkovitz 1982): (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
164. Replacement pattern of incisors and canines: (0) More than one replacement; (1) One replacement; (2) No replacement. ***Necrolestes*: (?) not preserved.**
165. Replacement of at least some functional molariform postcanines: (0) Present; (1) Absent. ***Necrolestes*: (0) Present. Comments.** The codification of *Necrolestes* follows the asseverations made by Goin *et al.,* (2007).
166. Procumbency and enlargement of the lower anterior-most incisor: (0) Absent; (1) Present (at least 50% longer than the adjacent incisor). ***Necrolestes*: (0) absent.**
167. Enlarged diastema in the lower incisor-canine region (better developed in older individuals): (0) Absent; (1) Present and behind the canine; (2) Present and behind the posterior incisor. ***Necrolestes*: (0) Absent.**
168. U-shaped ridge in the lower multi-rowed molars: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
169. Single-aligned and the labial row of multi-cusp or multi-rowed lower molar - Cusp ratio: (0) Second mesial cusp (b2 of Butler 2000) highest; (1) Mesial cusp highest. ***Necrolestes*: (?) not applicable.**
170. Multi-rowed upper premolar/molar - cusp ratio in the labial row of multi-cusp row: (0) Distal cusp highest, with a gradient of anteriorly decreasing height; (1) Cusps in same row of equal height. ***Necrolestes*: (?) Not applicable.**
171. Alignment of multi-cuspate upper first and second molars: (0) Second lingually offset from the first so that the lower second molar lingual row occludes with the lingual side of the upper second labial row; (1) Lower second molar labial row occludes with the labial side of the upper second labial row. ***Necrolestes*: (?) Not applicable.**
172. Enamel microstructure: (0) Synapsida columnar enamel (prismless); (1) 'Transitional' (sheath indistinct, 'prismatic' crystallites inclined at less than 45º to the 'interprismatic' matrix); (2) Full prismatic enamel; (3) Enamel absent. ***Necrolestes*: (1) Transitional. Coments:** Asher *et al.* (2007) distinguished two different enamel patterns in the longitudinal section of *Necrolestes* teeth. The inner zone consists of radial enamel with the prisms inclined about 40º apically, clearly showing the "Transitional" morphology.
173. Open root end of the postcanines (0) Absent; (1) Present. ***Necrolestes*: (0) absent.**

Vertebrae and Ribs

174. Fusion of the atlas neural arch and intercentrum: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
175. Atlas rib: (0) Present; (1) Absent. ***Necrolestes*: (?) Unknown.**
176. Fusion of dens to the axis: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**
177. Axis rib: (0) Present; (1) Absent (rib fused to form the transverse process). ***Necrolestes*: (?) Unknown.**
178. Postaxial cervical ribs: (0) Unfused; (1) Fused. ***Necrolestes*: (1) Fused.**
179. Number of thoracic vertebrae: (0) 13 or less; (1) 15 or more. ***Necrolestes*: (?) unknown.**
180. Overlapping ventral costal plates: (0) Absent; (1) Present. ***Necrolestes*: (?) unknown.**
181. Overlapping lumbar or posterior thoracic ribs: (0) Present; (1) Absent. ***Necrolestes*: (?) unknown.**
182. Anticlinal vertebra: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**
183. Mobile lumbar ribs: (0) Present; (1) Absent.

***Necrolestes*: (?) unknown.**

184. Orientation of lumbar ribs or transverse processes: (0) Posterolaterally directed; (1) Laterally or anterolaterally directed. ***Necrolestes*: (?) unknown.**
185. Xenarthrous articulation in addition to the pre- and post-zygapophyses of lumbar vertebrae: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**

Shoulder Girdle

186. Interclavicle: (0) Present; (1) Absent. ***Necrolestes*: (?) unknown.**
187. Contact relationships between the interclavicle (embryonic membranous element) and the sternal manubrium (embryonic endochondral element): (0) Two elements distinct from each other, posterior end of the interclavicle abuts with the anterior border of manubrium; (1) Two elements distinct from each other, the interclavicle broadly overlaps the ventral side of the manubrium; (2) Complete fusion of the embryonic membranous and endochondral elements resulting in a single and enlarged manubrium. ***Necrolestes*: (?) unknown.**
188. Inverclavicle distal expansion: (0) Absent; (1) Present. ***Necrolestes*: (?) unknown.**
189. Cranial margin of the interclavicle/manubrium: (0) Emarginated or flat; (1) With a median process. ***Necrolestes*: (?) unknown.**
190. Interclavicle to sternal manubrium length ratio (0) Interclavicle twice the length of manubrium; (1) Interclavicle nearly equal to manubrium in length. ***Necrolestes*: (?) unknown.**
191. Sternoclaviclular joint: (0) Immobile; (1) Mobile. ***Necrolestes*: (?) unknown.**
192. Sternal manubrial craniolateral process: (0) Absent; (1) Present. ***Necrolestes*: (?) unknown.**
193. Acromioclavicular joint: (0) Extensive articulation; (1) Limited articulation (either pointed acromion, pointed distal end of clavicle, or both). ***Necrolestes*: (?) unknown.**
194. Curvature of the clavicle: (0) Boomerang-shaped; (1) Slightly curved. ***Necrolestes*: (?) unknown.**
195. Scapula - supraspinous fossa: degree of development along the length: (0) Present only in the "acromional region" of the scapula, and on the cranial (dorsal) border of the scapula and positioned anterior to the glenoid); (1) Weakly developed (present only along a part of the scapula and positioned lateral to the glenoid); (2) Fully developed (present along the entire dorsal border of the scapula). ***Necrolestes*: (?) unknown.**
196. Proportion of supraspinous vs. infraspinous fossae (width measured across the "saddle region" of the spine, or near the mid-length of the scapula): (0) Supraspinous "fossa" on the cranial aspect of the scapula and much narrower than infraspinous fossa; (1) Supraspinous width is 50% to 80% that of infraspinous fossa; (2) Fossae subequal; (3) Supraspinous over 150% that of infraspinous fossa. ***Necrolestes*: (1).**
197. Scapula - acromion process: (0) Short stump, level with or behind the glenoid; (1) Hook-like and extending below the glenoid. ***Necrolestes*: (?) Unknown.**
198. Scapula - a distinctive fossa for the teres major muscle on the lateral aspect of the scapular plate: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**
199. Procoracoid: (0) Present; (1) Fused to the sternal apparatus. ***Necrolestes*: (?) Unknown.**
200. Procoracoid foramen: (0) Present; (1) Absent. ***Necrolestes*: (?) Unknown.**
201. Coracoid: (0) Large, with posterior process; (1) Small, without posterior process. ***Necrolestes*: (1) Small.**
202. Anterior process of the coracoid: (0) Indistinctive; (1) Distinctive; (2) Distinctive and forming a broad plate. ***Necrolestes*: (0) indistinctive.**
203. Coracoid process bridging over posteriorly toward the vertebral border of scapula (or fused with the latter): (0) Absent; (1) Present. ***Necrolestes*: (?) unknown.**
204. Size of the anterior-most element ('manubrium') relative to the subsequent sternebrae in the sternal apparatus: (0) Large; (1) Small. ***Necrolestes*: (?) unknown.**
205. Orientation ('facing' of the articular surface) of the glenoid (relative to the plane or the long axis of the scapula): (0) Nearly parallel and facing posterolaterally; (1) Oblique and facing more posteriorly; (2) Perpendicular. ***Necrolestes*: (?) Unknown.**
206. Shape and curvature of the glenoid: (0) Saddle-shaped, oval and elongate; (1) Uniformly concave and more rounded in outline. ***Necrolestes*: (1) concave.**
207. Medial surface of the scapula: (0) Convex; (1) Flat. ***Necrolestes*: (1) flat.**
208. Suprascapular incisure (defined as the prominent emargination on the cranial border of the supraspinus fossa): (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

Forelimb and Manus

209. Humeral head: (0) Subspherical, weakly inflected; (1) Spherical, strongly inflected. ***Necrolestes*: (1) Spherical, strongly inflected.**
210. Intertubercular groove of the humerus: (0) Shallow and broad; (1) Narrow and deep. ***Necrolestes*: (1) Narrow and deep.**
211. Size of the lesser tubercle of the humerus relative to the greater tubercle: (0) Wider; (1) Narrower. ***Necrolestes*: (1) Narrower.**
212. Torsion between the proximal and distal ends of the humerus: (0) Strong (≥30º); (1) Moderate (30º - 15º); (2) Weak. ***Necrolestes*: (0) Strong.**
213. Ventral extension of the deltopectoral crest or the position of the deltoid tuberosity: (0) Short and limited to the proximal part of the humeral shaft; (1) Extending ventrally (distally) at least 1/3 the length of the shaft. ***Necrolestes*: (1) Extending to at least 1/3 of the shaft.**
214. Teres tuberosity on medial side of humerus. (0) Absent; (1) Present; (2) Hypertrophied. ***Necrolestes*: (0) absent.**
215. Ulnar articulation on the distal humerus: (0)

Bulbous ulnar condyle; (1) Cylindrical trochlea in posterior view with a vestigial ulnar condyle in anterior view; (2) Cylindrical trochlea without an ulnar condyle (cylindrical trochlea extending to the anterior/ventral side). ***Necrolestes*: (1) vestigial ulnar condyle.**

216. Radial articulation on the distal humerus: (0) Distinct and rounded radial condyle in both anterior (ventral) and posterior (dorsal) aspects (that does not form a continuous synovial surface with the ulnar articulation in the ventral/anterior view of the humerus); (1) Rounded radial condyle anteriorly but cylindrical posteriorly; (2) Capitulum (forming a continuous synovial surface with the ulnar trochlea; cylindrical in both anterior and posterior aspects). ***Necrolestes*: (0) Condyle.**
217. Entepicondyle and ectepicondyle of the humerus: (0) Robust; (1) Weak. ***Necrolestes*: (1).**
218. Sigmoidal shelf for the supinator ridge extending proximally from the ectepicondyle: (0) Absent; (1) Present. ***Necrolestes*: (1) present.**
219. Coronoid process of semilunar notch of ulna: (0) Absent; (1) Present and level to olecranon process; (2) Present and higher than olecranon process. ***Necrolestes*: (0) Present and level to olecranon process.**
220. Styloid process of the radius: (0) Weak; (1) Strong. ***Necrolestes*: (1) Strong.**
221. Enlargement of the scaphoid: (0) Not enlarged (scaphoid ≤150% of the lunate); (1) Enlarged (scaphoid twice the size of the lunate); (2) Enlarged with a distolateral process. ***Necrolestes*: (?) Unknown.**
222. Size and shape of the hamate (unciform): (0) About equal size to the triquetrum, anteroposteriorly compressed; (1) Hypertrophied, much larger than the triquetrum, mediolaterally compressed. ***Necrolestes*: (?) Unknown.**
223. Trapezium morphology and proportion: (0) Elongate to cuboidal, larger than or subequal to the trapezoid; (1) Bean-shaped or fusiform, smaller than the trapezoid. ***Necrolestes*: (?) Unknown.**
224. Triquetrum-lunate proportion: (0) Triquetrum nearly twice the size of the lunate; (1) Triquetrum subequal to the lunate. ***Necrolestes*: (?) Unknown.**

Pelvic Girdle (12 characters)

225. Anterior process of the ilium: (0) Short (less than the diameter of the acetabulum); (1) Long, 1-1.5 times the diameter of the acetabulum; (2) Elongate, more than 1.5 times the diameter of the acetabulum. ***Necrolestes*: (?) unknown.**
226. Posterior process of the ilium: (0) Present; (1) Reduced or absent. ***Necrolestes*: (?) unknown.**
227. Acetabular dorsal emargination: (0) Open (emarginated); (1) Closed (with a complete rim). ***Necrolestes*: (1) Closed.**
228. Sutures of the ilium, ischium, and pubis within the acetabulum: (0) Present; (1) Fused. ***Necrolestes*: (0) Present.**
229. Ischiatic dorsal margin and tuberosity: (0) Dorsal margin concave (emarginated) and ischiatic tuberosity present; (1) Dorsal margin concave and ischiatic tuberosity hypertrophied; (2) Dorsal margin straight and ischiatic tuberosity small. ***Necrolestes*: (?) unknown.**
230. Posterior spine of the ischium: (0) Short and pointed; (1) expanded with oblique posterior spine; (2) expanded and truncated. ***Necrolestes*: (?) unknown.**
231. Epipubic bone: (0) Present; (1) Absent. ***Necrolestes*: (?) unknown.**
232. Width of epipubis: (0) Narrow; (1) wide. ***Necrolestes*: (?) unknown.**
233. Fusion of the sacral vertebrae with the proximal caudal vertebrae: (0) Absent; (1) Present. ***Necrolestes*: (?) unknown.**
234. Fusion of the ischium with the caudal vertebrae: (0) Absent; (1) Present. ***Necrolestes*: (?) unknown.**
235. Preacetabular tubercle on the ilium for M. rectus femoris: (0) Absent; (1) Present. ***Necrolestes*: (?) unknown.**
236. Fully encircled synovial surface inside the acetabulum: (0) Absent; (1) Present ***Necrolestes*: (?) unknown.**
237. Lesser psoas tuberosity or process on the pubis: (0) Absent; (1) Present. ***Necrolestes*: (?) unknown.**

Hindlimb and Pes (49 characters)

238. Inflected head of the femur set off from the shaft by a neck: (0) Neck absent and head oriented dorsally; (1) Neck present, head spherical and inflected medially. ***Necrolestes*: (0) Absent.**
239. Fovea for the acetabular ligament on the femoral head: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
240. Orientation of the greater trochanter: (0) Directed dorsolaterally; (1) directed dorsally. ***Necrolestes*: (?) not applicable.**
241. Position of the lesser trochanter: (0) On medial side of the shaft; (1) On the ventromedial or ventral side of the shaft. ***Necrolestes*: (?) not applicable.**
242. Size of the lesser trochanter: (0) Large; (1) Small to absent. ***Necrolestes*: (1) absent.**
243. The third trochanter of femur: (0) Absent; (1) Present; (2) Present as a continuous ridge connected to the greater trochanter. ***Necrolestes*: (0) Absent.**
244. Patellar facet ('groove') of the femur: (0) Absent; (1) Shallow and weakly developed; (2) Well-developed. ***Necrolestes*: (1) Shallow and weakly developed.**
245. Proximo-lateral tubercle or tuberosity of the tibia: (0) Large and hook-like; (1) Indistinct. ***Necrolestes*: (?) unknown.**
246. Distal tibial malleolus: (0) Weak; (1) Distinctive. ***Necrolestes*: (?) Unknown.**
247. Fibula contacting the distal end of the femur: (0) Present; (1) Absent; (2) Fibula fused with the tibia. ***Necrolestes*: (0) Present.**
248. Fused distal portions of the tibia and fibula: (0) Absent; (1) Present. ***Necrolestes*: (?) unknown.**

249. Parafibular process of the fibula: (0) Absent or unfused to the fibular; (1) fused to fibula and enlarged: ***Necrolestes*: (?) unknown.**
250. Distal fibular styloid process: (0) Weak or absent; (1) Distinct. ***Necrolestes*: (?) Unknown.**
251. Fibula contacting the calcaneus: (0) Extensive contact; (1) Reduced; (2) Absent. ***Necrolestes*: (?) Unknown.**
252. Superposition (overlap) of the astragalus over the calcaneus (lower ankle joint): (0) Little or absent; (1) Weakly developed; (2) Present. ***Necrolestes*: (1) Weakly developed.**
253. Astragalo-navicular articulation: (0) articulating facet indistinctive; (1) Weakly developed. ***Necrolestes*: (?) Unknown.**
254. Astragalar neck basal width (justification for separating this character from the navicular facet expansion is that the latter concerns symmetry, whereas this character deals with proportion; the distributions of these two character are different in some stem eutherians and crown marsupials): (0) Neck narrower than the head; (1) Neck about same width as the head (with parallel sides, constricted posterior to navicular facet); (2) Widest point of neck at mid-length (widening is not developed near the base of the neck); (3) Astragalar neck widest at the base. ***Necrolestes*: (2).**
255. Astragalonavicular contact aspect ratio: (0) Navicular contact transversely wider than dorsoventrally thick; (1) Navicular contact dorsoventrally thicker than transversely wide. ***Necrolestes*: (?) Unknown.**
256. Expansion of navicular contact in the astragalar head region: (0) Restricted anteriorly; (1) Asymmetrical spread only to the medial side of the astragalar "headneck region"; (2) Astragalar head supersedes navicular so the navicular facet shifted ventrally; (3) Symmetrical spread of the navicular facet to both the lateral and the medial sides of the neck (symmetrical with regards to the main axis of the neck). ***Necrolestes*: (?) Unknown.**
257. Astragalar trochlea (defined as a saddle-shaped upper ankle joint): (0) Absent; (1) Present, but weak (defining crest on the medial astragalo-tibial facet weakly developed); (2) Present, with clear separation of the medial and lateral tibial facets. ***Necrolestes*: (1).**
258. Well-defined medio-tibial crest (more or less parallel to the tibio-fibular crest) on the astragalus: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**
259. Astragalar medial plantar tuberosity: (0) Absent; (1) Present, but weakly developed; (2) Present, and ventrally flaring or protruding. ***Necrolestes*: (?) Unknown.**
260. Distal end of the calcaneal tubercle: (0) Short, dorso-ventrally compressed, without a terminal swelling; (1) dorso-ventrally compressed, with a terminal swelling; (2) Elongate, vertically deep, and mediolaterally compressed, with terminal swelling. ***Necrolestes*: (?) Unknown.**
261. Morphology of the peroneal process of the calcaneus: (0) Laterally expanded shelf, larger than the combined length of the sustentacular and astragalar facets, lateral to the astragalar facet; (1) With a distinct and long peroneal process, laterally projecting; (2) With a distinct peroneal process, demarcated by a deep peroneal groove at the base; (3) Laterally directed, small peroneal shelf demarcated from the anterior (cuboidal) edge of the calcaneus; (4) Anterolaterally directed, hypertrophied peroneal process/shelf; (5) Peroneal structure laterally reduced (lateral surface is straight from the calcaneal tubercle). ***Necrolestes*: (?) Unknown.**
262. Placement of the base of the peroneal process relative to the level of the cuboid facet of the calcaneus: (0) Peroneal structure posterior to the level of the cuboid facet; (1) Peroneal structure developed anteriorly at the same level as the cuboid facet; (2) Peroneal structure hypertrophied, extending anteriorly beyond the level of the cuboid facet. ***Necrolestes*: (?) Unknown.**
263. Peroneal groove of the calcaneus: (0) Indistinct, on the anterolateral aspect of the lateral shelf; (1) Distinct, deep separation of the peroneal process; (2) Weakly developed, with shallow groove on the lateral side of the process; (3) Distinct, on the anterolateral corner of the peroneal process. ***Necrolestes*: (?) Unknown.**
264. Alignment of the cuboid to the main axis of the calcaneus (horizontal plane): (0) On the anterior (distal) end of the calcaneus (the cuboid is aligned with the long axis of the calcaneus); (1) On the anteromedial aspect of the calcaneus (the cuboid is skewed to the medial side of the long axis of the calcaneus): ***Necrolestes*: (?) Unknown.**
265. Orientation of the calcaneocuboid joint in dorsoventral plane: (0) Calcaneocuboid facet on the calcaneus oriented ventrally (more visible in the plantar view than in dorsal view); (1) Calcaneocuboid facet oriented anteriorly (distally); (2) Calcaneocuboid facet oriented ventromedially or medio-obliquely. ***Necrolestes*: (?) Unknown.**
266. Saddle-shaped calcaneocuboid joint: (0) Calcaneocuboid facet on the calcaneus relatively flat to slightly concave; (1) Saddleshaped (differentiation of dorsal vs. proximal calcaneocuboid "facets" so that the whole calcaneocuboidal joint is saddle-shaped). ***Necrolestes*: (?) Unknown.**
267. Lower ankle joint - orientation of the sustentacular facet of the calcaneus in relation to the horizontal plane: (0) Nearly vertical; (1) Oblique ($\leq$70o) to nearly horizontal. ***Necrolestes*: (?) Unknown.**
268. Antero-posterior placement of the sustentacular facet relative to the astragalar facet on the calcaneus: (0) Directly anterior to the astragalar facet and vertically oriented on the medial edge of the calcaneus; (1) On the dorsal aspect and positioned anteromedial to the astragalar facet on the calcaneus; (2) On the dorsal aspect, medial to the astragalar facet; (3) On the dorsal aspect, anterior to the astragalar facet. ***Necrolestes*: (?) Unknown.**
269. Confluence of the sustentacular facet and the astragalar facet on the calcaneus: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

270. Ventral outline of the sustentacular process of the calcaneus: (0) Indistinctive; (1) Medially directed shelf, with rounded outline; (2) Protruding triangle, posteromedially directed; ***Necrolestes*: (?) Unknown.**
271. Antero-posterior position of the sustentacular facet/process (using the most salient point of the facet/process in ventral view as landmark) relative to the length of the calcaneus: (0) Near the midpoint; (1) Near the anterior (proximal) one-third. ***Necrolestes*: (?) Unknown.**
272. Shape of posterior calcaneo-astragalar process/protuberance and its contiguous fibular contact (if the fibula contact is present) on the calcaneus: (0) Confluent with fibular contact and indistinctive (best viewed medially); (1) Oblong to ellipsoidal; (2) Nearly spherical and bulbous, more transversely developed than character state 1; (3) Transversely confluent with the sustentacular facet. ***Necrolestes*: (?) Unknown.**
273. Placement of the CAF structure (structure of the calcaneoastragalar contact): (0) On the medial side of the body of the calcaneus; (1) On the dorsal side of the body of the calcaneus, but bordering on the body's medial margin (without a protruding outline); (2) On the dorsal side of the body of the calcanues and protruding beyond the body's medial margin; (3) Withdrawn and separated from the medial margin and placed along the lateral margin of the body of the calcaneus. ***Necrolestes*: (?) Unknown.**
274. Anterior ventral (plantar) tubercle of the calcaneus: (0) Absent; (1) Present, at the anterior edge (just lateral to the cuboid facet); (2) Present, set back from the anterior edge. ***Necrolestes*: (?) Unknown.**
275. Anteroventral groove or depression of the calcaneus: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**
276. Cross-sectional shape of the body of the calcaneus at the level of the posterior calcaneoastragalar facet: (0) Dorso-ventrally compressed; (1) Mediolaterally compressed. ***Necrolestes*: (?) Unknown.**
277. Ventral curvature of the calcaneal tubercle: (0) Present; (1) Absent. ***Necrolestes*: (?) Unknown.**
278. Proportion of the navicular and cuboid (transverse width measured in dorsal view): (0) Navicular narrower than or subequal to cuboid; (1) Navicular wider than cuboid. ***Necrolestes*: (?) Unknown.**
279. Proportion of the entocuneiform, mesocuneiform, and ectocuneiform (in ventral view): (0) Mesocuneiform and ectocuneiform small, their combined width smaller than the width of the entocuneiform; (1) Mesocuneiform and ectocuneiform large, their combined width (in dorsal view) exceeding the width of the entocuneiform. ***Necrolestes*: (?) Unknown.**
280. Medio-plantar aspect of the cuboid deeply notched by the peroneus longus tendon: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**
281. Prehallux: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**
282. Side-by-side contact of metatarsal V and the peroneal process of the calcaneus: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**
283. Relationships of the proximal end of metatarsal V to the cuboid: (0) Metatarsal V is off-set to the medial side of the cuboid; (1) Metatarsal V is so far offset to the side of the cuboid that it contacts the calcaneus; (2) Metatarsal V is level with the anterior end of the cuboid. ***Necrolestes*: (?) Unknown.**
284. Ventrolateral tubercle at the proximal end of metatarsal V: (0) Absent; (1) Present, at the anterior edge of the calcaneus; (2) Present, off-set posteriorly from the anterior edge of the calcaneus. ***Necrolestes*: (?) Unknown.**
285. Angle of metatarsal III to the calcaneus (which indicates how much the sole of the foot is 'bent' from the long axis of the ankle): (0) Metatarsal III aligned with (or parallel to) the long axis of the calcaneus; (1) Metatarsal III arranged obliquely from the long axis of the calcaneus. ***Necrolestes*: (?) Unknown.**
286. Metatarsal II and metatarsal III proximal ends: (0) II and III even or II more proximal than III; (1) III more proximal than II. ***Necrolestes*: (?) Unknown.**
287. Opposable hallux: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

Other Postcranial Characters

288. Ossified patella: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**
289. Sesamoid bones in the digital flexor tendons: (0) Absent; (1) Present, unpaired; (2) Present, paired. ***Necrolestes*: (2) Present, paired.**
290. External pedal (tarsal) spur: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**
291. Pes digital grouping: (0) Didactylous; (1) Syndactylous. ***Necrolestes*: (?) Unknown.**
292. Epiphyses in long bones: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**

Basicranium

293. External size of the cranial moiety of the squamosal: (0) Narrow; (1) Broad; (2) Expanded posteriorly to form the skull roof table. ***Necrolestes*: (0) Narrow.**
294. Participation of the cranial moiety of the squamosal in the endocranial wall of the braincase: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
295. Multiple vascular foramina (for rami temporales) in the squamosal and parietal: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
296. Multiple vascular foramina (for branches of external ethmoidal artery) in the dorsal surface of the frontal: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
297. Topographic relationships of the dentary-squamosal contact (or glenoid) and the cranial moiety of the squamosal (only applicable to taxa with the dentary-squamosal joint; this character is best seen in ventral view): (0) Contact on the internal aspect of the zygoma, without a constricted neck;

(1) Contact on the zygoma, with a constricted neck; (2) Contact on the cranial moiety of squama; (3) On zygoma, without a constricted neck. ***Necrolestes*: (?) Unknown.**

298. Cross-section profile of the squamosal anterior to its zygomatic root: (0) Rounded or triangular and tapering anteriorly; (1) Dorsoventral expanded and mediolaterally compressed, and not tapering anteriorly. ***Necrolestes*: (0).**

299. Postglenoid depression on the squamosal: (0) Present as the post-craniomandibular joint sulcus ("external auditory meatus" on the zygoma); (1) Absent; (2) Present on the skull base. ***Necrolestes*: (1) Absent.**

300. Squamosal - entoglenoid process: (0) Absent or vestigial; (1) Present, but separated from the postglenoid process; (2) Present, enlarged and connected to the postglenoid process. ***Necrolestes*: (?) Unknown.**

301. Position of the craniomandibular joint: (0) Posterior or lateral to the level of the fenestra vestibuli; (1) Anterior to the level of the fenestra vestibuli. ***Necrolestes*: (0) *Peligrotherium*, *Cronopio*: (0)**

302. Orientation of the glenoid on the squamosal: (0) On the inner side of the zygoma and facing ventromedially; (1) On the platform of the zygoma and facing ventrally. ***Necrolestes*: (1).**

303. Postglenoid process of the squamosal: (0) Absent; (1) Postglenoid crest raised below the fossa, but without a distinctive process; (2) Distinctive process; (3) Distinctive process buttressed by ectotympanic. ***Necrolestes*: (1).**

304. Postglenoid foramen position: (0) Posterior to the glenoid area; (1) Medial to the postglenoid process; (2) Anterior to the postglenoid process. ***Necrolestes*: (1) Medial.**

305. Postglenoid foramen presence vs. absence and composition: (0) Absent; (1) Present, in the squamosal; (2) Present, between the squamosal and petrosal; (3) Present, between the squamosal and ectotympanic. ***Necrolestes*: (3).**

306. Medial margin of the glenoid fossa: (0) Formed by the squamosal; (1) Formed by the alisphenoid. ***Necrolestes*: (?) Unknown.**

307. Squamosal - epitympanic recess (this character may be ordered): (0) No contribution to the "epitympanic area" of the petrosal; (1) Small contribution to the posterolateral wall of the epitympanic recess; (2) Large contribution to the lateral wall of the epitympanic recess; (3) Squamosal forming a large part of enlarged epitympanic sinus. ***Necrolestes*: (1) Small.**

308. Contribution of the basisphenoid wing (parasphenoid ala) to the external bony housing of the cochlea: (0) Participates in the rim of the fenestra vestibuli; (1) Does not reach the rim of the fenestra vestibuli; (2) Absent or excluded from the cochlear housing. ***Necrolestes*: (?) Unknown.**

309. Relationship of the cochlear housing to the lateral lappet of the basioccipital: (0) Entirely covered by the basioccipital; (1) Medial aspect covered by the basioccipital; (2) Partially (~about half width on the medial side) covered by the basioccipital; (3) Fully exposed as the promontorium. ***Necrolestes*: (?) Unknown.**

310. Thickened rim of the fenestra vestibuli: (0) Present; (1) Absent. ***Necrolestes*: (0) Present.**

311. Cochlear housing fully formed by the petrosal: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**

312. Ventromedial surface of the promontorium: (0) Flat; (1) Inflated and convex. ***Necrolestes*: (1) Inflated and convex.**

313. Lateral wall and overall external outline of the promontorium: (0) Triangular, with a steep and slightly concave lateral wall; (1) Elongate and cylindrical; (2) Bulbous and oval shaped. ***Necrolestes*: (2) Oval shaped.**

314. Cochlea: (0) Cochlear recess (without a canal); (1) Short canal; (2) Elongate canal, to the fullest extent of the promontorium; (3) slightly curved; (4) Elongate and partly coiled; (5) Elongate and coiled to at least 360°. ***Necrolestes*: (5) Elongate and coiled to at least 360°.**

315. Internal acoustic meatus - cribriform plate: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

316. Internal acoustic meatus depth: (0) Deep with thick prefacial commissure; (1) Shallow with thin prefacial commissure. ***Necrolestes*: (1) Shallow.**

317. Primary bony lamina within the cochlear canal: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

318. Secondary bony lamina for the basilar membrane within the cochlear canal: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

319. Crista interfenestralis: (0) Horizontal, broad, and extending to the base of the paroccipital process; (1) Vertical, delimiting the back of the promontorium; (2) Horizontal, narrow, and connecting to the caudal tympanic process. ***Necrolestes*: (?) Unknown.**

320. Post-promontorial tympanic recess: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**

321. Rostral tympanic process of the petrosal: (0) Absent or low ridge; (1) Tall ridge, but restricted to the posterior half of the promontorium; (2) Well-developed ridge reaching the anterior pole of the promontorium. ***Necrolestes*: (1) tall ridge.**

322. Caudal tympanic process of the petrosal: (0) Absent; (1) Present; (2) Present, notched; (3) Present, hypertrophied and buttressed against the exoccipital paracondylar process. ***Necrolestes*: (1) Present.**

323. Petrosal - tympanic process: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

324. Rear margin of the auditory region: (0) Marked by a steep wall; (1) Extended onto a flat surface. ***Necrolestes*: (?) Unknown.**

325. Prootic canal: (0) Absent; (1) Present, vertical; (2) Present, horizontal and reduced. ***Necrolestes*: (2) Present, horizontal and reduced.**

326. Position of the sulcus for the anterior distributary of the transverse sinus relative to the subarcuate fossa. (0) Anterolateral; (1) Posterolateral. ***Necrolestes*: (?) Unknown.**

327. Lateral trough floor anterior to the tympanic aperture of the prootic canal and/or the primary facial foramen: (0) Open lateral trough, no bony floor; (1) Bony floor present; (2) Lateral trough absent. ***Necrolestes*: (0) no bony floor.**
328. Anteroventral opening of the cavum epiptericum: (0) Present; (1) Present, with reduced size (due to the anterior expansion of the lateral trough floor); (2) Present, partially enclosed by the petrosal; (3) Present, enclosed by the alisphenoid and petrosal; (4) Present, as large piriform fenestra. ***Necrolestes*: (?) Unknown.**
329. Enclosure of the geniculate ganglion by the bony floor of the petrosal in the cavum supracochleare: (0) Absent; (1) Present. ***Necrolestes*: (1) present.**
330. Hiatus Fallopii: (0) Present, in the petrosal roof of the middle ear; (1) Present, at the anterior end of the petrosal; (2) Absent (applicable only to those taxa with a cavum supracochleare). ***Necrolestes*: (1) Present.**
331. Foramen ovale - composition: (0) Between the petrosal and alisphenoid; (1) Secondary foramen partially or fully enclosed by the alisphenoid, in addition to the primary foramen between the petrosal and alisphenoid; (2) In the petrosal (anterior lamina); (3) Between the alisphenoid and squamosal; (4) Within the alisphenoid. ***Necrolestes*: (?) Unknown.**
332. Foramen ovale - position: (0) On the lateral wall of the braincase; (1) On the ventral surface of the skull. ***Necrolestes*: (?) Unknown.**
333. Number of exit(s) for the mandibular branch of the trigeminal nerve (V3): (0) One; (1) Two. ***Necrolestes*: (?) Unknown.**
334. Quadrate ramus of the alisphenoid: (0) Forming a rod underlying the anterior part of the lateral flange; (1) Absent. ***Necrolestes*: (?) Unknown.**
335. Alisphenoid canal (for the ramus inferior and/or ramus infraorbitalis): (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**
336. Anterior lamina exposure on the lateral braincase wall: (0) Present; (1) Reduced or absent. ***Necrolestes*: (?) Unknown.**
337. Orientation of the anterior part of the lateral flange: (0) Horizontal shelf; (1) Ventrally directed; (2) Medially directed and contacting the promontorium; (3) Vestigial or absent. ***Necrolestes*: (?) Unknown.**
338. Vertical component of the lateral flange ('L-shaped' and forming a vertical wall to the pterygoparoccipital foramen): (0) Present; (1) Absent. ***Necrolestes*: (?) Unknown.**
339. Vascular foramen in the posterior part of the lateral flange (and anterior to the pterygoparoccipital foramen): (0) Present; (1) Absent. ***Necrolestes*: (?) Unknown.**
340. Relationship of the lateral flange to the crista parotica (or the anterior paroccipital process that bears the crista): (0) Widely separated; (1) Narrowly separated; (2) Continuous. ***Necrolestes*: (?) Unknown.**
341. Pterygoparoccipital foramen (for the ramus superior of the stapedial artery): (0) Laterally open notch; (1) Foramen enclosed by the petrosal or squamosal; (2) Absent. ***Necrolestes*: (?) Unknown.**
342. Position of the pterygoparoccipital foramen relative to the level of the fenestra vestibuli: (0) Posterior or lateral; (1) Anterior. ***Necrolestes*: (?) Unknown.**
343. "Bifurcation of the paroccipital process" - presence vs. absence (this is modified from the character used in several previous studies): (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**
344. Posterior paroccipital process of the petrosal: (0) No ventral projection below the level of the surrounding structures; (1) Projecting below the surrounding structures. ***Necrolestes*: (0).**
345. Morphological differentiation of the anterior paroccipital region: (0) Anterior paroccipital is bulbous and distinctive from the surrounding structures; (1) Anterior paroccipital region has a distinct crista parotica. ***Necrolestes*: (1) Distinct crista parotica.**
346. Epitympanic recess lateral to the crista parotica: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**
347. Tympanohyal contact with the cochlear housing: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**
348. Relationship of the squamosal to the paroccipital process: (0) Squamosal covers the entire paroccipital region; (1) No squamosal cover on the anterior paroccipital region; (2) Squamosal covers a part of the paroccipital region, but not the crista parotica (the squamosal wall and the crista parotica are separated by the epitympanic recess). ***Necrolestes*: (2) Epitympanic recess.**
349. Medial process of the squamosal reaching toward the tympanic cavity: (0) Absent; (1) Present (near or bordering on the foramen ovale). ***Necrolestes*: (?) Unknown.**
350. Stapedial artery sulcus on the petrosal: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
351. Transpromontorial sulcus for the internal carotid artery on the cochlear housing: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
352. Deep groove on the anterior pole of the promontorium: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**
353. Perbullar canal or sulcus for the internal carotid artery. (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**
354. Epitympanic wing medial to the promontorium: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**
355. Ectopterygoid process of the alisphenoid: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**
356. Tympanic process of the alisphenoid: (0) Absent; (1) Present, but limited to the "piriform" region of the basicranium; (2) Intermediate; (3) Well-developed, extending to near the jugular foramen. ***Necrolestes*: (0) Absent.**
357. Hypotympanic recess in the junction of the alisphenoid, squamosal, and petrosal: (0) Absent; (1)

Present. ***Necrolestes*: (?) Unknown.**

358. Separation of the fenestra cochleae from the jugular foramen: (0) Absent; (1) Separate but within the same depression; (2) Separate (not within the same depression). ***Necrolestes*: (1) Separate but within the same depression.**
359. Channel of the perilymphatic duct: (0) Open channel and sulcus; (1) At least partially enclosed channel. ***Necrolestes*: (1).**
360. Jugular foramen size relative to the fenestra cochleae (applicable only to those taxa with a jugular foramen fully separated from the fenestra cochleae): (0) Jugular subequal to the fenestra cochleae; (1) Jugular larger than the fenestra cochleae. ***Necrolestes*: (0) subequal.**
361. Relationship of the jugular foramen to the opening of the inferior petrosal sinus: (0) Confluent; (1) Separate. ***Necrolestes*: (1) Separate.**
362. Stapedial muscle fossa size: (0) Absent; (1) Present, small; (2) Present, large (twice the size of the fenestra vestibuli). ***Necrolestes*: (2) Present, large.**
363. Alignment of the stapedial fossa relative to the crista interfenestralis: (0) aligned with crista interfenestralis; (1) lateral to the crista interfenestralis ***Necrolestes*: (1) lateral.**
364. Hypoglossal foramen: (0) Indistinct, either confluent with the jugular foramen or sharing a depression with the jugular foramen; (1) Separated from the jugular foramen; (2) Separated from the jugular foramen; the latter has a circular, raised external rim. ***Necrolestes*: (?) Unknown.**
365. Number of separate hypoglossal foramina: (0) Single; (1) Double. ***Necrolestes*: (?) Unknown.**

Middle Ear Ossicle Characters

366. Geometry (shape) of the incudo-mallear contact: (0) Trochlear (convex and cylindrical) surface of the incus; (1) Trough; (2) Saddleshaped contact on the incus; (3) Flat surface. ***Necrolestes*: (?) Unknown.**
367. Alignment of the incus and the malleus: (0) Posterior-anterior; (1) Posteromedial to anterolateral; (2) Dorsoventral. ***Necrolestes*: (?) Unknown.**
368. Twisting of the dorsal plate relative to the trochlea on the quadrate: (0) Dorsal plate aligned with the trochlea; (1) Dorsal plate twisted relative to the trochlea, (2) Dorsal plate twisted and elevated from the trochlea; (3) Dorsal plate reduced to a conical process (crus longum). ***Necrolestes*: (?) Unknown.**
369. Presence of a quadrate/incus neck (slightly constricted region separating the dorsal plate or crus brevis from the trochlea; this represents the differentiation between the 'body' and crus brevis of the incus): (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**
370. Dorsal plate (= crus brevis) of the quadrate/incus: (0) Broad plate; (1) Pointed triangle; (2) Reduced. ***Necrolestes*: (?) Unknown.**
371. Incus - angle of the crus brevis to crus longum of the incus (this is equivalent to the angle between the dorsal plate and the stapedial process of the quadrate): (0) Alignment of the stapedial process (crus longum) and the dorsal plate (crus brevis) (or an obtuse angle between the two structure) (distinctive process is lacking, stapes/incus contact is on the medial side of the quadrate trochlea); (1) Perpendicular or acute angle of the crus brevis and crus longum ("A-shaped" incus). ***Necrolestes*: (?) Unknown.**
372. Primary suspension of the incus/quadrate on the basicranium: (0) By quadratojugal in addition to at least one other basicranial bone; (1) By squamosal only; (2) By petrosal (either by the preserved direct contact of the incus or by inference from the presence of a well-defined crista parotica). ***Necrolestes*: (2) well-defined crista parotica.**
373. Quadratojugal: (0) Present; (1) Absent. ***Necrolestes*: (1) Absent.**
374. Morphology of the stapes: (0) Columelliform-macroperforate; (1) Columelliform-imperforate (or microperforate); (2) Bicrurate-perforate. ***Necrolestes*: (?) Unknown.**
375. Stapedial ratio: (0) Less than 1.4; (1) 1.4-1.8; (2) ≥1.8. ***Necrolestes*: (1) 1.4-1.8.**
376. Bullate stapedial footplate: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**
377. Malleolar neck: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**
378. Length of the malleus manubrium: (0) Shorter than the combined width of the surangular and prearticular anterior to the incudomalleolar joint; (1) longer than the combinted width of surangular and prearticular. ***Necrolestes*: (?) Unknown.**
379. Thickness of malleolar manubrium: (0) robust; (1) gracile. ***Necrolestes*: (?) Unknown.**
380. Distinctive angle or bending of Meckel's bone (=anterior portion of postdentary rod) anterior to the level of ectotympanic (angular) bone: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**
381. Medio-lateral contact vs. separation of Meckel's element (either independent or as an ossified component of the "postdentary rod") from the posterior (pterygoid) region of mandible: (0) Presence of medio-lateral contact either in adult or in embryonic stage until Meckel's cartilage re-absorption; (1) Embryonic Meckel's cartilage medio-laterally separated from the posterior part of mandible; (2) Ossified Meckel's cartilage medio-laterally separated from the posterior part of mandible: ***Necrolestes*: (?) Unknown.**
382. Ectotympanic size/shape (may be ordered): (0) Plate-like; (1) Curved and rod-like; (2) Ring-shaped; (3) Slightly expanded (fusiform); (4) Expanded; (5) Tube-like. ***Necrolestes*: (?) Unknown.**
383. Ectotympanic arc (0) about 70 degrees: (1) ≤ 90 - 135 degrees; (2) ≥ 135 degrees. ***Necrolestes*: (?) Unknown.**
384. Anterior process of the ectotympanic (angular): (0) Present; (1) Absent. ***Necrolestes*: (?) Unknown.**
385. Position/orientation of the incisura tympanica: (0) Posteroventral; (1) Posterior; (2) Postero-dorsal;

(3) Dorsal. ***Necrolestes*: (?) Unknown.**

386. Fusion of the ectotympanic to other bones: (0) Absent; (1) Fused to other bones. ***Necrolestes*: (?) Unknown.**

387. Entotympanic and its contribution to the bullar structure: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

Other Cranial Characters (48 characters)

388. Posterior extent of the bony secondary palate: (0) Anterior to the posterior end of the tooth row; (1) Level with the posterior end of the tooth row; (2) Extending posterior to the tooth row; (3) Extending to the basisphenoid-basioccipital suture. ***Necrolestes*: (1) Level with the posterior end of the tooth row.**

389. Posterior median spine (or torus) on the palate: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**

390. Pterygopalatine ridges: (0) Present; (1) Absent. ***Necrolestes*: (?) Unknown.**

391. Transverse process of the pterygoid: (0) Present and massive; (1) Present but reduced (as the hamulus); (2) Greatly reduced (with a vestigial crest on pterygoid) or absent. ***Necrolestes*: (?) Unknown.**

392. Pterygoids contact on midline on pharyngeal roof: (0) Present; (1) Absent. ***Necrolestes*: (?) Unknown.**

393. Ventral opening of the minor palatine foramen: (0) Encircled by the pterygoid (and ectopterygoid if present) in addition to the palatine; (1) Encircled by the palatine and maxilla, separated widely from the subtemporal margin; (2) Encircled completely by the palatine (or between palatine and maxilla), large, with thin bony bridge from the subtemporal margin; (3) Large, posterior fenestration; (4) Notch. ***Necrolestes*: (?) unknown.**

394. Transverse canal foramen: (0) Absent; (1) Present. ***Necrolestes*: (1) Present.**

395. Carotid foramen position: (0) Within the basisphenoid; (1) Within the basisphenoid/basioccipital suture; (2) Within the basisphenoid/petrosal suture; (3) Through the opening of the cavum epiptericum. ***Necrolestes*: (2).**

396. Overhanging roof of the orbit: (0) Absent; (1) Present, formed by the frontal. ***Necrolestes*: (1) Present.**

397. Exit(s) of the infraorbital canal: (0) Single; (1) Multiple. ***Necrolestes*: (0) Single.**

398. Composition of the posterior opening of the infraorbital canal (maxillary foramen): (0) Between the lacrimal, palatine, and maxilla; (1) Exclusively enclosed by the maxilla; (2) Enclosed by the maxilla, frontal and palatine. ***Necrolestes*: (0).**

399. Size and shape of the lacrimal: (0) Small, oblong-shaped on the facial part of the rostrum; (1) Large, triangle-shaped on the facial portion of rostrum; (2) Crescent shaped on the facial portion of the rostrum; (3) Reduced to a narrow strap; (4) Absent from the facial portion of the rostrum. ***Necrolestes*: (?) Unknown.**

400. Location of the lacrimal foramen: (0) Within the orbit; (1) On the facial side of the lacrimal (anterior to or on the anterior orbital margin). ***Necrolestes*: (0) within the orbit.**

401. Number of lacrimal foramina: (0) One; (1) Two. ***Necrolestes*: (0) one.**

402. Lacrimal foramen composition: (0) Within the lacrimal; (1) Bordered by or within the maxilla. ***Necrolestes*: (?) Unknown.**

403. Maximum vertical depth of the zygomatic arch relative to the length of the skull (this character is designed to indicate the robust vs. gracile nature of the zygomatic arch): (0) Between 10-20%; (1) Between 5-7%; (2) Zygoma incomplete. ***Necrolestes*: (1) 5-7%.**

404. Ultimate upper molar implanted in the anterior root of zygoma. (0) Absent. (1) Present. ***Necrolestes*: (1) Present.**

405. Frontal/alisphenoid contact: (0) Dorsal plate of the alisphenoid contacting the frontal at the anterior corner; (1) Dorsal plate of the alisphenoid with more extensive contact with the frontal (~50% of its dorsal border); (2) Absent. ***Necrolestes*: (?) Unknown.**

406. Frontal-maxilla facial contact: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

407. Nasal-frontal suture - medial process of the frontals wedged between the two nasals: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

408. Posterior width of the nasal bones: (0) Narrow; (1) broader than the width at the mid-length of the nasal. ***Necrolestes*: (1).**

409. Pila antotica: (0) Present; (1) Absent. ***Necrolestes*: (?) Unknown.**

410. Fully ossified medial orbital wall of the orbitosphenoid: (0) Absent; (1) Present, forming the ventral floor of the braincase but not the entire orbital wall; (2) Present, forming both the braincase floor and the medial orbital wall. ***Necrolestes*: (0) Absent.**

411. Separation of the optic foramen from the sphenorbital fissure: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

412. Exit for maxillary nerve: (0) Separate from sphenorbital fissure, behind alisphenoid; (1) Separate from sphenorbital fissure, within alisphenoid; (2) Confluent with sphenorbital fissure. ***Necrolestes*: (?) Unknown.**

413. Separate anterior opening of orbitotemporal canal: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

414. Orbital opening for the minor palatine nerve: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

415. Anterior part of the jugal on the zygoma: (0) Anterior part of the jugal extends to the facial part of the maxilla and forms a part of the anterior orbit; (1) Anterior part of the jugal does not reach the facial part of the maxilla and is excluded from the anterior orbit margin. ***Necrolestes*: (?) Unknown.**

416. Posterior part of the jugal: (0) Contributes to the squamosal glenoid; (1) Borders on but does not contribute to the squamosal glenoid; (2) Terminates anterior to the squamosal glenoid. ***Necrolestes*:**

(?) Unknown.

417. Maxillary in the sub-temporal margin of the orbit: (0) Absent; (1) Present; (2) Present and extensive. ***Necrolestes*: (?) Unknown.**

418. Orbital process of the frontal borders on the maxilla within orbit: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**

419. Anterior ascending vascular channel (for the arteria diploëtica magna) in the temporal region: (0) Open groove; (1) Partially enclosed in a canal; (2) Completely enclosed in a canal or endocranial; (3) Absent. ***Necrolestes*: (?) Unknown.**

420. Posttemporal canal for the arteria and vena diploëtica: (0) Present, large; (1) Small; (2) Absent. ***Necrolestes*: (?) Unknown.**

421. Nuchal crest: (0) Overhanging the concave or straight supraoccipital; (1) Weakly developed with convex supraoccipital. ***Necrolestes*: (?) Unknown.**

422. Sagittal crest: (0) Prominently developed; (1) Weakly developed; (2) Absent. ***Necrolestes*: (2) Absent.**

423. Tabular bone: (0) Present; (1) Absent. ***Necrolestes*: (?) Unknown.**

424. Occipital slope: (0) Occiput sloping posterodorsally (or vertically oriented) from the occipital condyle; (1) Occiput sloping anterodorsally from the occipital condyle (such that the lambdoidal crest is leveled anterior to the occipital condyle and condyle is fully visible in dorsal view of the skull). ***Necrolestes*: (0).**

425. Occipital artery groove on the occiput extending dorsal to the posttemporal foramen: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

426. Foramina on the dorsal surface of the nasals: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

427. Septomaxilla: (0) Present, with the ventromedial shelf; (1) Present, without the ventromedial shelf; (2) Absent. ***Necrolestes*: (2) Absent.**

428. Internarial process of the premaxilla: (0) Present; (1) Absent. ***Necrolestes*: (?) Unknown.**

429. Posterodorsal process of the premaxilla: (0) Does not extend beyond canine ("short or absent"); (1) Extends beyond canine ("intermediate"); (2) Contacts frontal posteriorly ("long"). ***Necrolestes*: (?) Unknown.**

430. Facial part of the premaxilla borders on the nasal: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

431. Premaxilla - palatal process relative to the canine alveolus: (0) Does not reach to the level of the canine alveolus; (1) Reaches the level of the canine alveolus. ***Necrolestes*: (1) premaxilla reaches canine alveolus.**

432. Incisive foramina size: (0) Small (one or two incisors); (1) Intermediate (three or four incisors); (2) Large (more than half the palatal length). ***Necrolestes*: (0) small.**

433. Palatal vacuities: (0) Absent; (1) Present, near palatomaxillary border; (2) Present, either positioned near or extended to the posterior edge of bony palate. ***Necrolestes*: (0) Absent.**

434. Major palatine foramina: (0) Absent; (1) Present. ***Necrolestes*: (0) Absent.**

435. Ossified ethmoidal cribriform plate of the nasal cavity: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

436. Posterior excavation of the nasal cavity into the bony sphenoid complex: (0) Absent; (1) Present; (2) Present and partitioned from the nasal cavity. ***Necrolestes*: (?) Unknown.**

Cranial Vault and Brain Endocast Characters (7 characters)

437. External bulging of the braincase in the parietal region: (0) Absent; (1) Expanded (the parietal part of the cranial vault is wider than the frontal part, but the expansion does not extend to the lambdoidal region); (2) Greatly expanded (expansion of the cranial vault extends to the lambdoidal region). ***Necrolestes*: (?) Unknown.**

438. Anterior expansion of the vermis (central lobe of the cerebellum): (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

439. Overall size of the vermis: (0) Small; (1) Enlarged. ***Necrolestes*: (?) Unknown.**

440. Lateral cerebellar hemisphere (excluding the paraflocculus): (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

441. External division on the endocast between the olfactory lobe and the cerebral hemisphere (well-defined transverse sulcus separating the olfactory lobes from the cerebrum): (0) Absence of external separation of the olfactory lobe from cerebral hemisphere; (1) Enlarged olfactory lobes; (2) Clear division of transverse sulcus. ***Necrolestes*: (?) Unknown.**

442. Encephalization quotient (0) Below 0.13; (1) Between 0.15-0.25, (2) Above 0.26. ***Necrolestes*: (?) Unknown.**

443. Expansion of the posterior cerebral hemisphere (for each hemisphere, not the combined width of the posterior hemispheres): (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

Soft-tissue characters

444. Trophoblasts in the placenta: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

445. Mullerian ducts (oviduct and uterus) pass in between the ureters: (0) Absent; (1) Present. ***Necrolestes*: (?) Unknown.**

Newly added characters

446. Proximal end of femur: (0) craniocaudally flattened; (1) subcircular in cross-section. ***Necrolestes*: (0) flattened.**

447. Trochanteric fossa (Asher *et al.*, 2007): (0) absent; (1) present. ***Necrolestes*: (0) absent.**

448. Coronoid ridge on dentary (Rougier *et al.*, 2009a): (0) subhorizontal or oblique; (1) close to vertical. ***Necrolestes*: (0).**

449. Upper molar series (Bonaparte & Migale, 2010): (0) sub-parallel; (1) labially convex and anteriorly convergent. ***Necrolestes*: (1) labially convex**

and anteriorly convergent.

450. Bulbous check-teeth with low and blunt cusps (Bonaparte, 2002): (0) cusps thin and acute; (1) present. ***Necrolestes*: (1) present.**

451. Molars: (0) brachyodont; (1) hypsodont-like. **Comment**: The molars are considered as hypsodont-like in taxa having very deep crowns and proportionally small occlusal areas, with small, reduced, or absent roots. *Leonardus, Cronopio*, and *Necrolestes* show transversally and mesiodiastally reduced crown that are proportionately tall, and which show extremely reduced or opened roots. ***Necrolestes*: (1) hypsodont-like.**

452. Upper molar root number (modified from Rougier *et al.,* 2011): (0) 3 or less; (1) with extra roots, more than 3. ***Necrolestes*: (0).**

453. Lower molar root contour (Rougier *et al.,* 2011): (0) subcilindrical in cross-section; (1) mesiodistally compressed and transversely wide, supporting the whole width of the crown. ***Necrolestes*: (1) mesiodistally compressed.**

454. Upper molars with posterior cingulum, stylocone, and posterior stylar cusp connected (Gelfo & Pascual, 2001): (0) separated; (1) present. ***Necrolestes*: (0) separated.**

455. Upper molars anterior and posterior cingula (Bonaparte, 1986): (0) reduced; (1) forming very wide platforms. ***Necrolestes*: (0) reduced.**

456. Upper molar cingula (Bonaparte, 1990; Gelfo & Pascual, 2001; Rougier *et al.,* 2011): (0) located at the base of the crown; (1) elevated and continuous with occlusal planes. ***Necrolestes*: (?) not applicable.**

457. Upper molars parastyle (Bonaparte, 1990): (0) straight or slightly curved; (1) hooked. ***Necrolestes*: (?) not applicable.**

458. Second crus commune (peculiar junction between the lateral and posterior semicircular canals at the point at which the latter passes under the former) (Ladevèze *et al.,* 2008): (0) absent; (1) present. ***Necrolestes*: (1) present.**

Appendix 2. Data matrix

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Haldanodon

Castorocauda

Hadrocodium

Shuotherium

Pseudotribos

Asfaltomylos

Ambondro

Ausktribosphenos

Bishops

Teinolophos

Steropodon

Obdurodon

Ornithorhynchus

Tachyglossus

Fruitafossor

Gobiconodon

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Akidolestes

1????10??00?20????1221001021140110011 1000000?1101000120113020112010001000004012200?0100???00??020?11???000??0??0000000?2000
220222100??00000001100??10110001000000000 1110?????0?????001100001001101121111111001110111110111010000121111201000011?000021010
1001000000010020100100011000010001210000 21010?001020??1???
??????????????????????????0??????10?0???2?????12?????????0???0????????????????000?00000000?

Spalacotherium

1111010??000202?????2100102114011001110 00000?1101000100113120012010001000004011200?0100???00??020?11???000??0??0000000?2000
220222100??0000000?????????10?000?0000000??10??????0???
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Maotherium

11?1010??0002020??122100102114010101110000000 1110 1001?0001311001201000100000 4011100?0100???00??020?11???000??0??0000000?2000
220222100??000000022?0??1010220000010000??10?????0?1?000011110??0?1?011211?11110?11101111101110100001211122000000 01?11002101
00001000000?13020100????11000010000200000 21010?00102??11?00?231111?????????1?????1????1?????0??1?????????2?00000????????1????????
?????????????????????????????22??100000???2???12?????????1??00?????????????????110000000000?

Zhangheotherium

11?1010??0002020??1221001?21140101011 10000000 1110 1001?000131100120100010000 04011100?0100???00??020?10???000??0??0000000?2000
220222100??00000002200??10102200000100001110????20?11000011110010011011211111110011101111101110100001211122000000 01?110021010
0001000000013020100100011000010000200000 2101????1020111?0012311112????1101001?1?1?10???0??1210111020000000001?0?1??1??????
21??????0??????0??????0??1?????10???0???2???12??2????????00????????????????110000000000?

Peramus

11?111110000 2021??1121010121030120011101100200002000?0001301001300010001000100 11[01]0002110000[01]?0121121?0?010000??00010020
200011022111100000000 2??????000003310?00??0???0??
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??0000000000?

Vincelestes

11?2?111000[01]2021??111101012113012001110000010 1000000?0001301001300000020000000110000210??000?0120?11?0?010000??0001012000
00110221100?00000000 3100000100333342000030??00??????0111100111101201?101?21101111001110101000 1110?000012101220000000 11100021
10001020?001001302010110001101 00?????210??0?001110020 20011?00123?112400?1110100101110100 10011[01]21111110201100000001100211 1???
???21?0????????????0101101000102010000010120001002020001001110 00000??1????????1101100000000

Nanolestes

11?101110000 2021??112?0??12103012001110??????0000000?0001301001300010021000100 1100002 1000?00?0121?11?0?0?0000??101201202000
11022111000000000011?????001?02??0?00??0???0?????0???
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??0?00000000?

Kielantherium
11?101110?002?21??111101?2????0130011?0??????0000000?0001301??13000110211001011102015110000[01]001??????????????????????????
?01?02221?1001000000????????0??12??0??0??????0?????0???
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??0000000000?

Aegialodon
???1?01??13000110211001?11102015110 0?11001????????????????????????????
1??2221?1001000000???????????????????????????????0??
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??00000000?

Montanalestes
11?2?13100004021??111201032103013001110??????120200100001 3?2??130102102110012012021151100111002???????????????????????????0
??02221?1001110000???????????03??0?00???
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???1??????????0??0?0?????

Prokennalestes
11?1113100001021??111201022103012001110 1[01]112?12020000200130220130201101110012012021151100111002210220200100110010110100200
012022212100111 0000???????1010033?0000?00?1?0?????0???
???2311125111110100102?10?????13?1?111011???11001???110?21????
????2??1??????????????????????0????????????1??????????1?????????????0??????????????0?000000000

Murtoilestes
???13022013?20210111001?012021151100?1100?210220200?001100101100002000
12?222121001?10000???????????????????????????????0??
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??00000000?

Eomaia
11?1113100001021??11120102210301200111010111112010000200130220130 20?10111001 2??202?151100111??2210220200100110010??000?20001
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0012210021223020101301111010000100210001200111?0?1????2??0????1??51?11??????????1??????????????????????????11????????????
???????????????0????????00??0??10?0???2???10?20???????02??1??????1??????????0?00000000?

Kennalestes
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2022212100111000021????01011[01]33200100001101?????001???
??????????????????2??????????????????????????????11002122112210223111 2511??210211002?1?2001013?????1011020100011001100211 0??
????21?2??????321300?0110200000200??0?010121211002022011100210 10?00??1011223???00000000000

Asioryctes
11?2?131000040211011120002210301300111011112201102000010013022013020210211001201203115110011100221022011010011001000000?20001
20222121001110000100000010111332101 0000?101?????001111??11110??????????????????????0?????0???0?11000?????2?0??00??????0??10
000122100212230201013011110100000?0200001?0011100212211221022311125?1??2102110?241?2001013???1110110201000110011002110??????
21?2??????32130020110200000200?101010?2121100202201110021010000??1011223??110000000000?

Ukhaatherium
?1???????00?40??????????022???0??00?1101112201102000020013022013020?102110012012031151100111?0221022011010011001000000?2000
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00012210021223020101301111010000???200??1??01??00?1?2???221???3?????????2???21????4?0????0???????1???????0?0?1??????21?1????
?????2???????21??0?0?????0????????0?010???21??0????????0??????0?????????????110000000000?

Zalambdalestes
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0?20001202221210011100002?11?001101133?1010200?111?????0??1110011110??0???01?221011110?2110111200221021000121112200000001?111
0211210?1221002122 3?201013?011300000000200001?001110031221122102231112 5?1??2102110024112001013???1110110201000110011002111?
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Daulestes
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202221210011100001?00??00101133200?0??0?100?????0???
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Aspanlestes
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1202221210011100 00???????????033?0??0????1?0?????0??
???3?????????1?0?0?1????0?????1??????????????00?1????????1????
???????1??????????????????????0???010000000?

Eoungulatum
?????1???????????????????1??????0???0?1??10110???????????0130242131103102110 01?112012151110012 00320?1223211103121001 0000?0100
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???????1???10000000?

Cimolestes
1??2?1010?0140211?111200?2210301 2?0111010122?11010000100130231130202102110012212031151100112002210121110100111 0000000?20001
2022212100111 00002?00??0000113321?00????1?0????20??
??0??????????????????
???0000000000?

Gypsonictops
1??2?101000140211?111200?22103012?0111011122?121200011001302311312021021100122120411511001120022101211101001110000000?20001
202221210011100 00??????0000113320?00????1?0????20??
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???0?00000000?

Protungulatum
11?2?101000140211?11120002210301200111010120?121100001001302421311021021100121120121511100120132 0?12232111031000000000?01001
20222121001110000??????0000113321?00????100????20???
????2220032122312?101301113201 1??????????????????????????????2311125?1??1?0?0?00??[01]0?????1?????????????11001????1??21????
???????2??1???????????????????????????0?10000000?

Erinaceus
11?2?1310001412110111200022103013001110101101121220010001302201311031021100101120221511100121122 0?1212211102 0??0000000?01003
302221211111100003200001010333342000200111 0????2011111001111 01200?1111211011110121101112002210210001211122 1?00000111112102101

2220032122512010130111320110000020010120011100312111201022311125111121021100231130011113???11101102011001100110021112131112122011101421300211113000002001101101121211?2212101110021110020122011223111100000000000

Leptictis

11?2?13100014021101112000221030130011101112211212200100013022213110310211001211204115110001101220?121111100111100000000?010012
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Canis

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Felis

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Rattus

1112?111000141211011112000222?011000210???????????????013???21313?0004000000????42041100013?1400??2022211020?????????0?00
3102???????01?0???4311112?2?333343???1?02112????201111100111101200?10112210111000110100021022112000012111211?001011111121110
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Oryctolagus

1112?111000140211011111000222?011?1121000120000100001??013???01313?0004000000????210410?00?3?1300??2012111030?????????0?013
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Bradypus

111??1310101412110111100022113013?01110????????????????0??????15???????????03??0
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Tamandua

111??1310101412110??????0?21?30???1??10?????????????????0???
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Glyptotherium

111??1310101412110111100022113013101111????????????????0??????15???????????03??0
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Dasypus

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Chaetophractus

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Euphractus

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Holoclemensia

?????????????????????????????????0?1???????????????????130210130201102110011111021151100?2100120?12011110001001001112120001
2?222121001000000??????????????????0?????????????0???
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Sinodelphys

11???131010?4021??111?0??2210301300111000??11?1010?00?001302??130101100110011111?21151100121??121122???110??????01101212100?
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00121201??1242202011021?210001111021000020011??0??
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Deltatheridium

11?2?14101012021??1111000421030130011100000110001000000013021013000110[123]11001111102115110001100121122010110001001001001022
201202221210010000001100??00002222211100?12100????20???
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Atokatheridium

?????????????????????????????????0?????????????????????1?021013000110011001?111021151100?0??0121?2201011000100100100102220
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???00000000?

Sulestes

?????????????????????????????????0?????????????????????13?21013000110011001?111121151100?111022112201011000100100111022201
2?2221210010100000??????????????????????????????0???
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??000000000?

Marsasia
11?2?14101012021??11112014??1?013?0?????????????????????13????130?02?0011001?11112115110?22112????????????????????????????0
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Asiatherium
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01????????2???????????????????????????0?001110?3020112010?2311125????1111?0??23??4101013?????10?1?2??0?0101111???11???????2
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Kokopellia
?1?1?1410?012??1??1?1100??2?????3?01110????1?000100000001302101301021021100100111221511011221022 1?220201100111?1001111021001
20222121001110000 1?????0000?222?1?10??0?100????20??
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??00000000?

Anchistodelphys
??????????????????????????????????0????????????????????01?02101302031021100 1?0111220511011321022112202212102101010111110?200
1202221110011100000?????????????????????????????0???
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Albertatherium
??????????????????????????????????0????????????????????0?3022013?????????????????1?????????????????2112202221102101100111112200
?2?222111??????000?????????????2??????????????????0???
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???00000000?

Didelphodon
11?2?14101011021??1111001421130 1?001110001???000110000001302201300031021100121111220512 01?3211221122022221020101002011022101
2022211100111100000????????0022222 1?00????1?0????20??
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Pediomys
???2?14101011021??11110014211301?001110???????????????0013022013010310211001111112205120113211221122022221021100001111 0210012
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Turgidodon
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?????????????????????????2???223111???0????0??0?1??11?????1??????1???????00?1?????0?11??????
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Mayulestes
11?2?14101014?211011110014210301300111000001100010000000130210130103102110011111122151201131102211220222200211000010110 22101
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Pucadelphys
11?2?14101014021101111001421030130011100000110001000000013021013120310211001011112215120113210221022022221121110002111121001
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1213011012422020110212210 11?11?0210??0?0011100302011201112311125 11??1101002124110101013?????10110210010100 11111111??????21?1
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Andinodelphys
11?2?14101014021101111001421030130011100000110001000000013021013120310211001211112215120103211221022022221121110002111121001
2022211100111000010000000002222211101 11?100?????0??????0???????0???0???0????
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21?1????????????02?111?1000021?010110 01201?1002031011000210111 1??21??????????0?00000000?

Didelphis
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0012130110124220211102123201111110210010200111003020112011123111251111111100212311[01]101013?????10110200000101111011111213111 2
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Marmosa
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1213011012422021110212220111111021001020011100302011201112311125111111110021231111 01013?????10110200000101111011111213111212101
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Caenolestes
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202221110011 1?00011000000000222221010020 2100???0?01111100111101201?10112310111101211111120022112121102111220000000111110 1110000
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Dasyurus
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Dromiciops
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Thylacomyidae
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Macropus

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Acrobates

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Phascolarctos

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0121302?11251002012 1213?10111110021001020112100302111001032311125111111130 02?2311410101 3?????10110200000102111011111 2131??211
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Vombatus

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Phalanger

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0121302?11251002012 1213?20111110021001020112100302111313032311125111111130 02?2311410101 3?????10110200000103111001111 2131??212
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Pseudocheirus

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Petauroides

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21111005213102011121000021101011001201010120321211002101112 0121???2230011000000000000

Perameles

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0121302?11251002012 1213?101111100200100201111003020112021123111251111111300 2?2311410101 3?????10110200000102111011111 2131??2111
0111004212002011121000021001011011201010020321210002111011012 1???2230011000000000000

Dryolestes

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??1???
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Henkelotherium

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Crusafontia

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Leonardus

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Mesungulatum

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Coloniatherium

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Reigitherium

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Paraungulatum

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???101?1111?

Groebertherium
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???10010001?

Peligrotherium
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?12??????????2???????????????2?????????????????0???????????????????0?1??[01]???????????????????0?10111110?

Amphitherium
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10221110000000001?00????0??000?0?00??
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???0000000000?

Cronopio
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220221110??010?000?3??0?01012233??01001?1100?????0??
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?????21[02]??????????????0???????????1???0?1011??????0????????????0[01]100?000??2??02?1????01001?0001

Necrolestes
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220222100??010?000100000010122333001001 0?0000?1?100?1?1???1??0??????????1????10???11?111010101111??????10?????????00??101??
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??21?11????????????11????12100?00?11???1?0????????0???2?0??2???1000???????????0001100100??1

Appendix 3. List of synapomorphies of selected nodes of the strict consensus tree

Cladotheria
Char. 7: 0→1 - Angular process of the dentary: Present, distinctive but not inflected.
Char. 30: 4→3 - Ventral (inferior) border of the dentary peduncle: Robust and short.
Char. 115: 0→1 - Stylar cuspule “B” (opposite the paracone): Small but distinctive.
Char. 148: 1→0 - Upper canine - presence vs. absence, and size: Present and enlarged.
Char. 150: 1→0 - Lower canine - presence vs. absence and size: Present and enlarged.
Char. 178: 0→1 - Postaxial cervical ribs: Fused.
Char. 254: 0→2 - Astragalar neck basal width: Widest point of neck at mid-length.
Char. 257: 0→1 - Astragalar trochlea: Present, but weak.
Char. 313: 1→2 - Lateral wall and overall external outline of the promontorium: Bulbous and oval shaped.
Char. 350: 0→1 - Stapedial artery sulcus on the petrosal: Present.
Char. 351: 0→1 - Transpromontorial sulcus for the internal carotid artery on the cochlear housing: Present.
Char. 362: 1→2 - Stapedial muscle fossa size: Present, large.

Dryolestoidea
Char. 65: 0→1 - Protoconid (cusp a) and metaconid (cusp c) height ratio nearly equal.
Char. 136: 0→1 - Development of the distal metacristid: absent.
Char. 151: 0→1 - Number of lower canine roots: two.
Char. 228: 1→0 - Sutures of the ilium, ischium, and pubis within the acetabulum present.
Char. 244: 2→1 - Patellar facet (‘groove’) of the femur: shallow and weakly developed.
Char. 325: 1→2 - Prootic canal present, horizontal and reduced.
Char. 458: 0→1 - Second crus commune present.

Dryolestidae
Char. 33: 1,2→3 - Tilting of the coronoid process of the dentary: coronoid process near vertical (95º to 105º).
Char. 52: 0→1 - Ultimate lower premolar - lingual cingulid: present.
Char. 56: 0→1 - Elongation of posterior premolars present.
Char. 153: 2→1 - Number of lower premolars: four.
Char. 154: 3→0 - Number of lower molars or molariform postcanines: six or more.
Char. 155: 3→0 - Number of upper molars or molariform postcanines: six or more.
Char. 156: 4→0 - Total number of upper postcanine loci: more than 8.
Char. 457: 0→1 - Upper molars parastyle hooked.

Meridiolestida
Char. 4: 1→2 - Degree of development of Meckel’s sulcus vestigial or absent.
Char. 13: 2→4 - Location of the mandibular foramen: not associated with any of the above structures.
Char. 21: 2→1 - Ventral border of the masseteric fossa present as a low and broad crest.
Char. 31: 0→1 - Gracile and elongate dentary peduncle present.
Char. 36: 1→0 - Alignment of the ultimate molar to the anterior margin of the dentary coronoid process: Ultimate molar medial to the coronoid process.
Char. 48: 0→1 - Ultimate lower premolar - arrangement of principal cusp a, cusp b, and cusp c: Distinctive

triangulation.
Char. 79: 1→2 - Orientation of the paracristid relative to the longitudinal axis of the molar: nearly transverse.
Char. 85: 1→0 - Morphology of the talonid of the molar: Absent.
Char. 104: 0→3 - Height and size of the paracone (cusp B) and metacone (cusp C): metacone absent.
Char. 121: 0→2 - Size and labial extent of the metastylar lobe and parastylar lobe: metastylar lobe much larger than the parastylar lobe.
Char. 152: 1→2 - Number of upper premolars: three.
Char. 159: 0→1 - Diastema separating the lower first and second premolars: Present, subequal to one tooth-root diameter or more.
Char. 299: 2→1 - Postglenoid depression on the squamosal absent.
Char. 450: 0→1 - Bulbous check-teeth with low and blunt cusps present.
Char. 453: 0→1 - Lower molar root contour: mesiodistally compressed and transversely wide, supporting the whole width of the crown.

Mesungulatoidea
Char. 62: 0→1 - Postcingulum present.
Char. 75: 0→1 - Postcingulid (distal transverse cingulid above the gum level) on the lower molars: Present, horizontal above the gum level.
Char. 79: 2→1 - Orientation of the paracristid (or the crest between cusps a and b) relative to the longitudinal axis of the molar: Oblique.

Node *Peligrotherium* + ((*Paraungulatum* + *Reigitherium*) + (*Coloniatherium* + *Mesungulatum*))
Char. 60: 1→0 - Postvallum/prevallid shearing (angle of the main trigonid shear facets, based on the second lower molar) absent.
Char. 124: 2→3 - Outline of the lower first molar crown (in crown view): Rectangular (or rhomboidal).
Char. 454: 0→1 - Upper molars with posterior cingulum, stylocone, and posterior stylar cusp connected: present.
Char. 455: 0→1 - Upper molars anterior and posterior cingula forming very wide platforms.
Char. 456: 0→1 - Upper molar cingula elevated and continuous with occlusal planes.